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CARL BLOMS BOKTRYCKERI A.-B.

Introduction

SHERRINGTON and his co-workers described and analysed a number of ipsilateral and crossed reflexes in decerebrate and spinal cats (and dogs). Subsequent electrophysiological work, mainly on ipsilateral reflexes, has aimed at disclosing the contributions from specified afferent systems and at revealing the neuronal paths for the effects.

The crossed reflexes to muscles can be classified in two main groups. One category are those evoked by limb movements and the other are those appearing with the ipsilateral flexion reflex. In the former group a number of reflexes have been described. The best known of these reflexes, Philippson's reflex, is a contraction of the contralateral knee extensors evoked by forced flexion at the opposite knee (PHILIPPSON 1905, SHERRINGTON 1908, 1909 a). Philippson's reflex is the crossed correlate to the ipsilateral lengthening reaction. Another crossed reflex with relaxation of knee extensors and contraction of knee flexors has been correlated with the ipsilateral shortening reaction (SHERRINGTON 1908, 1909 a). A detailed description of crossed reflexes evoked by flexion or extension of the hip or ankle has also been given by SHERRINGTON (1908, 1909 a).

Of the crossed reflexes appearing with the ipsilateral flexion reflex the most frequent reaction is contraction of hip, knee and ankle extensors and relaxation of the antagonist flexors (SHERRINGTON 1906, 1910). More seldom there is crossed flexion with contraction of flexors and relaxation of extensors (GRAHAM BROWN 1911, 1912, 1914, GRAHAM BROWN and SHERRINGTON 1912). Characteristic differences between the ipsilateral flexion reflex and the crossed extension reflex were described by LIDDELL and SHERRINGTON (1923 a, b, cf. CREED, DENNY-BROWN, ECCLES, LIDDELL and SHERRINGTON, 1932).

It is now known that reflexes can be mediated by two routes, either 'directly' to alpha motoneurones or indirectly via the gamma-loop (cf. GRANIT 1955). HUNT (1951) has found that crossed actions are exerted on gamma motoneurones. Hence crossed reflexes may be evoked via the gamma-loop, but the crossed reflexes discussed above were also found after interruption of the gamma-loop by de-afferentation on the testing side.

As described above SHERRINGTON correlated the crossed reflexes evoked from muscles with the ipsilateral reflexes. It is now assumed that the ipsilateral shortening reaction is caused by impulses in I a afferents (with annulo-spiral endings on muscle spindles) and the lengthening reaction by impulses in I b afferents (from Golgi tendon organs) (cf. GRANIT 1955, ECCLES 1957, LUNDBERG 1959, LLOYD 1960, HUNT and PERL 1960). If the crossed correlates of these reflexes were evoked from the same afferent systems their reflex actions would be in agreement with the scheme of double reciprocal organization. In a recent electrophysiological investigation PERL (1958) examined the crossed effect of volleys in group I muscle afferents and has suggested that the crossed actions from the I a and I b systems of knee extensors and flexors are organized in a double reciprocal fashion. Support for this view was reached in experiments with adequate stimulation of muscles (PERL 1959).

The aim of the present work was to investigate further the actions by volleys in somatic myelinated afferents on contralateral alpha motoneurones and the supraspinal control of these crossed paths. Preliminary reports of the results have been given (HOLMQVIST 1960, 1961).

Methods

The experiments were performed on unanaesthetized cats. During the operation ether mixed with suitable amounts of O_2 and air was given but at least 2—3 hours elapsed between the withdrawal of anaesthesia and the beginning of the experiment. In some experiments the blood pressure was continuously measured. If there were signs of vascular failure a solution of Dextran was given intravenously. The cats were paralyzed with Flaxedil and artificially respirated.

Two main types of preparations were used. One type was decerebrated by intercollicular section. In these experiments the cerebellum was sometimes removed by suction in order to expose the brain stem to permit subsequent lesions in the lower pons. The lesions were made with a spatula 3 mm wide, as described by HOLMQVIST and LUNDBERG (1961). To obtain a low spinal preparation the cord was transected in Th_{12}—L_2. The other type of preparation was cats made spinal (L_1 or L_2) under aseptical conditions 10—40 days before the final experiment. These cats developed lively spinal reflexes. The classical flexor reflex as well as the crossed extensor reflex could easily be elicited and many cats in addition showed stepping reflexes. A few of these chronic spinal cats were decerebrated in the final experiment but in most of them the carotid arteries (external carotid, lingual, internal carotid, occipital and ascending pharyngeal arteries) were ligated bilaterally in order to deprive the cerebrum of some of its blood supply (VOORHOEVE 1960). These preparations were easier to maintain in a good condition than the decerebrated ones.

The experimental procedure used for investigating crossed reflex actions was similar to that used in investigations on ipsilateral actions (ECCLES and LUNDBERG 1959 a, b). Both hindlimbs were denervated with exception of some hip muscles. The action of conditioning volleys was tested on contralateral monosynaptic reflex discharges recorded from the cut ventral roots. On the conditioning side the ventral roots were usually left intact. In order to obtain a larger and more adjustable monosynaptic reflex, two test volleys were often used. The first volley was subliminal for reflex discharge, and preceded the second by an interval giving maximal facilitation of the

monosynaptic reflex evoked by the second volley (ECCLES and LUNDBERG 1959 b). It was always controlled that there remained an adequate subliminal fringe. In a few cats the crossed actions were tested without laminectomy on monosynaptic reflex discharges evoked and recorded in the peripheral muscle nerves. The recording electrodes were placed peripherally to the stimulating ones. To obtain the monosynaptic reflex the stimulus strength was adjusted to activate a maximal amount of I a fibres without activating efferents antidromically.

Two techniques were employed to record the effect of conditioning volleys. Either the monosynaptic test reflex discharge was recorded at 10—15 fixed intervals after the conditioning volley, or many test reflexes were scattered at all intervals after the conditioning volley and superimposed in one exposure. With the former method interaction curves at several conditioning strengths were obtained by plotting the height of the conditioned monosynaptic reflex expressed in percentage of the height of the unconditioned test reflex with time along the abscissa. Each value was obtained from the mean of 10 superimposed records taken at a frequency of about 1/sec (cf. for example Fig. 1). With the other technique about 100—200 monosynaptic reflex discharges were superimposed in one exposure. Conditioning volleys were given at a fixed interval after the sweep start. At each successive sweep the monosynaptic reflex discharge was automatically delayed so that the test reflex was made to traverse the screen. This procedure was repeated 3—5 times. The CRO spot brightness was kept very weak for the baseline and was increased during the discharges. In parallel on another beam an 'integrated' curve was recorded, which consisted of more or less confluencing spots, each spot recorded simultaneously with a monosynaptic reflex discharge. To obtain this curve the monosynaptic discharge was passed through an 'integrating' network with a time constant chosen to avoid the recording of spontaneous fluctuations of short duration in the height of the monosynaptic discharges. Hence short lasting effects evoked by the conditioning volley are not recorded and these curves can only serve as a complement to the picture given by the monosynaptic discharges. It should also be noted that the time constant of the circuit leads to a displacement in time of the effect on the 'integrated' curve in comparison with the effect on the monosynaptic discharges. The direction of this displacement depends on whether the monosynaptic reflexes have been automatically delayed along the time axis (from left to right on the records, cf. Fig. 6) or in the opposite direction (cf. Fig. 3). Both techniques have been employed as two apparatuses with these different characteristics have been used. Another difference between these apparatuses is the distribution of the discharges on the screen, one giving an equal (cf. Fig. 3)

dispersion across the screen the other not (cf. Fig. 4). The apparatuses have been constructed by Mr E. EIDE.

Special care was taken to disclose from which afferent fibre system crossed actions could be evoked. Thus series were always taken with fine gradation of conditioning stimulus strength, expressed as multiples of the threshold strength for the nerve if not otherwise mentioned. When a train of conditioning volleys was given, the stimulus strength was kept the same for all impulses. The incoming conditioning volleys were recorded in the entry zone of the dorsal roots. When the group I actions were investigated, discriminative tests were regularly performed to examine the threshold separation between the fast and slow component of group I fibres (BRADLEY and ECCLES 1953, ECCLES, ECCLES and LUNDBERG 1957) and always used to decide the maximal group I strength. This double volley test was performed in immediate connection to the series investigated.

For stimulation condensor discharges (half time decay 45 μsec) were used. C-fibres were not activated by these stimuli.

The nerves supplying the following muscles were used and the abbrevations given below will stand for them:

Q =quadriceps (including all components)
V-Cr =vastus lateralis, vastus medialis and crureus
R =rectus
Gr =gracilis
BSt =posterior biceps and semitendinosus
G =gastrocnemius and soleus
med.G=medial gastrocnemius
Pl =plantaris
FDL =flexor digitorum longus and flexor hallucis longus
DP =extensor digitorum longus and tibialis anterior

In addition:

Sur =the sural nerve
Joint =the posterior knee joint nerve
FRA =flexor reflex afferents; group II and III muscle afferents, high threshold joint afferents and skin afferents (ECCLES and LUNDBERG 1959 a).

The abbrevations *i* and *c* will be used in the illustrations and stand for *ipsilateral* and *contralateral*.

The term *leg* will be used to denote the part of the hindlimb between the knee and ankle joints.

Low threshold muscle afferents denotes group I muscle afferents and *high threshold muscle afferents* group II and III muscle afferents.

The term *double reciprocal innervation* will be used to denote contralateral actions of opposite effect to the ipsilateral ones. SHERRINGTON (1909 b) did not use the term entirely in this sense.

Chapter I

The result of ventral root stimulation on contralateral motoneurones

Activity in motoneurones are known to influence motor nuclei located in the same and adjacent segments via the recurrent collaterals (RENSHAW 1941, ECCLES, FATT and KOKETSU 1954, WILSON 1959). In the present investigation it was of importance to find out whether impulses in alpha efferents were also capable of influencing contralateral motoneurones.

The curves in Fig. 1 refer to an experiment on an acute low spinal cat. On either side the monosynaptic reflex from BSt, recorded in the S_1 ventral root, was conditioned by single volleys in the contralateral combined L_7 and S_1 ventral roots at a strength maximal for the alpha efferents. There was not a trace of an effect (□, ▲) whereas the usual long lasting Renshaw inhibition appeared with conditioning of the ipsilateral L_7 ventral root (×, ●). Similar findings were made on test reflexes from the G nerve.

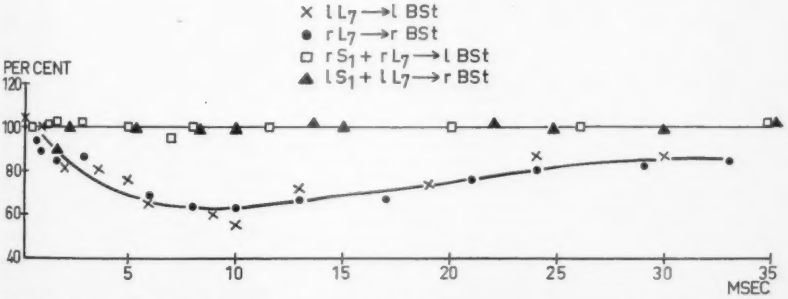

Fig. 1. Effects of single conditioning volleys in the ventral L_7 root or the combined ventral L_7 and S_1 roots on the monosynaptic reflexes from the BSt nerve in combinations between the left (l) and right (r) side as indicated by the table of signs. In each instance 100 % on the ordinate represents the unconditioned amplitude of the test reflexes. Conditioned amplitudes of monosynaptic test reflexes, expressed as percentage of control amplitudes, are plotted as a function of the time interval between incoming conditioning and testing volleys which were recorded at the dorsal root entry zone. Acute spinal (L_2) cat.

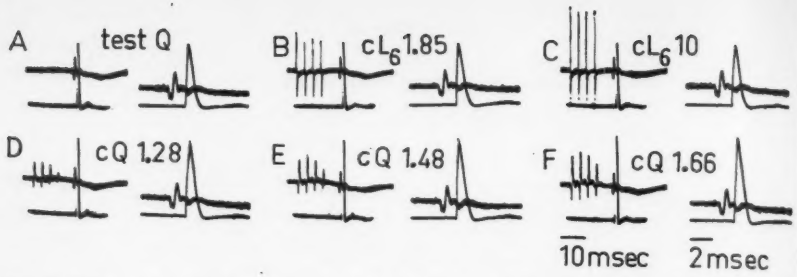

Fig. 2. Effects of a train of conditioning volleys in the ventral L_6 root (B and C) and in the Q nerve (D—F) on the Q monosynaptic test reflexes recorded in the ventral root on the contralateral side. The unconditioned test reflexes are shown in A. The conditioning stimulus strengths relative to the threshold strength for the root and nerve are indicated in the records. In each record the right traces were obtained simultaneously at faster sweep speed to show the height of the monosynaptic reflexes (lower traces) while the left traces show the time relation between the testing and conditioning incoming volleys recorded in the dorsal root entry zone (upper traces). The ventral roots L_5—S_1 were cut bilaterally. All records were obtained from about 10 superimposed traces. Chronic spinal cat.

Experiments were also made on chronic spinal cats, 2—6 weeks after transection of the cord, and in these experiments a train of stimuli was given to the ventral roots. Neither under these circumstances were there any effects on contralateral monosynaptic test reflexes as is illustrated in Fig. 2 where the Q test reflexes were recorded in the L_6 ventral root (shown unconditioned in A) and conditioned with 4 volleys in the contralateral L_6 ventral root (B and C). In Fig. 2 the actions are illustrated only at one interval from a series. The stimulus strength of 1.85 times threshold for the ventral root (B) was chosen in order to activate the alpha fibres and 10 times threshold for activating the gamma fibres (C) (LEKSELL 1945). For comparison the lower row (D—F) shows the crossed actions by a similar train of impulses activating low threshold muscle afferents. This action must be mediated through the dorsal roots as the ventral L_5—S_1 roots were cut. The finding that there are no actions on contralateral motoneurones from antidromic activation of efferent fibres gives the methodological advantage that it is not necessary to section the ventral roots on the conditioning side when investigating the crossed effect of volleys in muscle afferents evoked by stimulation of a muscle nerve.

Summary

In spinal cats antidromic volleys in efferent fibres had no effect on contralateral motoneurones tested on their monosynaptic reflex discharges.

Chapter II

Crossed spinal actions from low threshold muscle afferents

Introduction

The only previous investigation with modern electrophysiological techniques on crossed group I effects is that by PERL (1958, 1959). On acute high spinal animals he found that small group I volleys from the V-Cr nerve inhibited contralateral V-Cr monosynaptic reflexes and at the same time facilitated the antagonist, the contralateral BSt reflexes. When the group I volley was increased, he found crossed facilitation of the V-Cr and inhibition of the BSt reflexes. A corresponding set of double reciprocal effects on BSt and V-Cr, respectively, were observed when conditioning the BSt nerve. PERL suggested that the actions evoked by low threshold volleys might be due to activity in group I a fibres and the additional actions by more high threshold afferents to I b impulses.

In the present investigation crossed group I effects were not found in acute spinal animals and in chronic low spinal animals it has usually been necessary to employ repetitive stimulation to reveal crossed group I actions. In section A the criteria are given by which effects can be ascribed to impulses in group I fibres. Section B deals with attempts to utilize the two components of the group I volley in this study of crossed connections. The pattern of crossed group I effects is described in section C.

Results

A. *Criteria for ascribing crossed effects by a train of volleys in muscle nerves to activity in group I muscle afferents*

In a series of experiments on acute low spinal animals with prominent crossed actions from high threshold muscle afferents (described in chapter III) no or uncertain crossed effects were observed on single or repetitive stimulation of muscle nerves at group I strength. The findings reported in this chapter were made on chronic spinal animals, 2—6 weeks after transection of the cord in the upper lumbar region. Even in these preparations single group I volleys had at most small crossed effects,

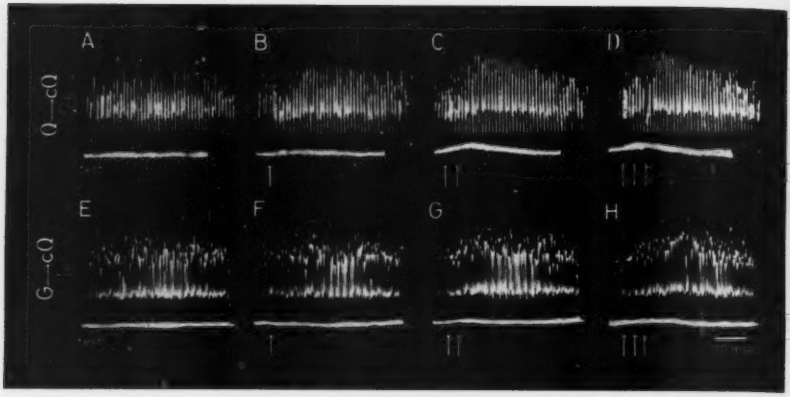

Fig. 3. Crossed actions on the Q monosynaptic test reflexes (shown unconditioned in A and E) evoked by one (B and F), two (C and G) and three (D and H) conditioning volleys in the Q nerve (B—D) and the G nerve (F—H) at maximal group I stimulus strength for the nerves (2.5 and 1.6 times threshold, respectively).
Each record consists of about 150 monosynaptic reflexes superimposed in one photographic exposure evoked at various intervals after the sweep start, while the conditioning stimuli were fixed in time. Arrows indicate time of arrival of the conditioning group I volleys recorded in the dorsal root entry zone. The lower trace is an integrated recording of the monosynaptic discharges. (Further explanation is given under methods.) Chronic spinal cat.

which could wax or wane and hence were difficult to analyse systematically. Repetitive stimulation was tried for conditioning and was found to be much more effective as is illustrated in Fig. 3. Records B—D show the effect of conditioning volleys in the Q nerve, and records F—H in the G nerve on contralateral Q monosynaptic test reflexes (shown unconditioned in A and E). The conditioning strengths 2.5 (B—D) and 1.6 (F—H) times threshold for respective nerves was just maximal for group I on single volley stimulation. In B a single conditioning volley in Q has some facilitatory effect but the effect increases considerably when two or three stimuli were given in C and D. On the other hand there is no visible effect by a single conditioning group I volley in the G nerve (F) but facilitation appears with two conditioning volleys (G) and increases with the addition of a third volley (H). In excitable preparations large effects were often found with a conditioning train of 2—3 volleys but the actions could sometimes be increased when 4—6 volleys were employed.

Under conditions when a single volley had no action the facilitatory effect evoked by the second volley appeared after a central delay which

could be very brief, less than 2 msec (cf. Fig. 3 G). This indicates a minimal pathway with two interneurones. The duration of action evoked by 2 to 3 volleys was usually 20—30 msec.

It is now necessary to discuss the criteria for ascribing these effects to group I afferents. Even with single conditioning volleys this may be difficult since there is an overlap in threshold between group I and II fibres but the usage of repetitive stimulation gives a further complication.

Fig. 4 illustrates the customary procedure of measuring the actions with graded conditioning stimulation. In each record is shown the effect of a conditioning train from the Q nerve on the contralateral Q test reflexes (upper traces) at the stimulus strength indicated and, immediately below, at the same sweep speed, the conditioning train triphasically recorded at the dorsal root entry zone. The lower traces in each record were obtained at faster sweep speed and are triphasic recordings of single volleys evoked at the strength indicated (left) and in combination with a supramaximal group I volley evoked in the refractory period of the first volley (right). In Fig. 4 facilitation appears already in record B at a stimulus strength of 1.14 times threshold, at which strength but a fraction of group I fibres are activated. The facilitation is marked in D at 1.36 times threshold when the first stimulus activates only somewhat more than half of the group I afferents. In G the strength of the first stimulus is almost maximal for group I but the increase in facilitation from D to G is comparatively small, and there is only a slight increase when the strength is raised above group I (H and I). With effects evoked by such small group I volleys as in Fig. 4 there can be little doubt that they are caused by impulses in group I afferents, if subthreshold temporal facilitation in group II fibres can be excluded.

For this purpose recordings were made from dorsal root filaments, as is illustrated in Fig. 5 with simultaneous recording from 2 filaments, containing one (lower trace) and two (upper trace) afferents respectively from soleus. A train of 4 stimuli was given to the soleus nerve. The stimulus strengths indicated are expressed as multiples of the threshold strength for the fastest conducting fibre. The three afferents conducted at velocities of 107, 94 (upper trace) and 66 m/sec (lower trace), which according to HURSH (1939) correspond to fibre diameters of 18, 16 and 11 μ. The two coarse fibres are in the group I range and the thin one in the group II range. The thresholds were 1.0 (A), 1.26 (E) and 1.79 (H) respectively. The fibres were regularly activated by all stimuli (at a frequency of 250/sec) at a strength of 1.26 (E), 1.49 and 2.21 times threshold respectively. It was found that with repetitive stimulation at the frequencies used group I and II fibres are recruited in essentially the same manner. When the

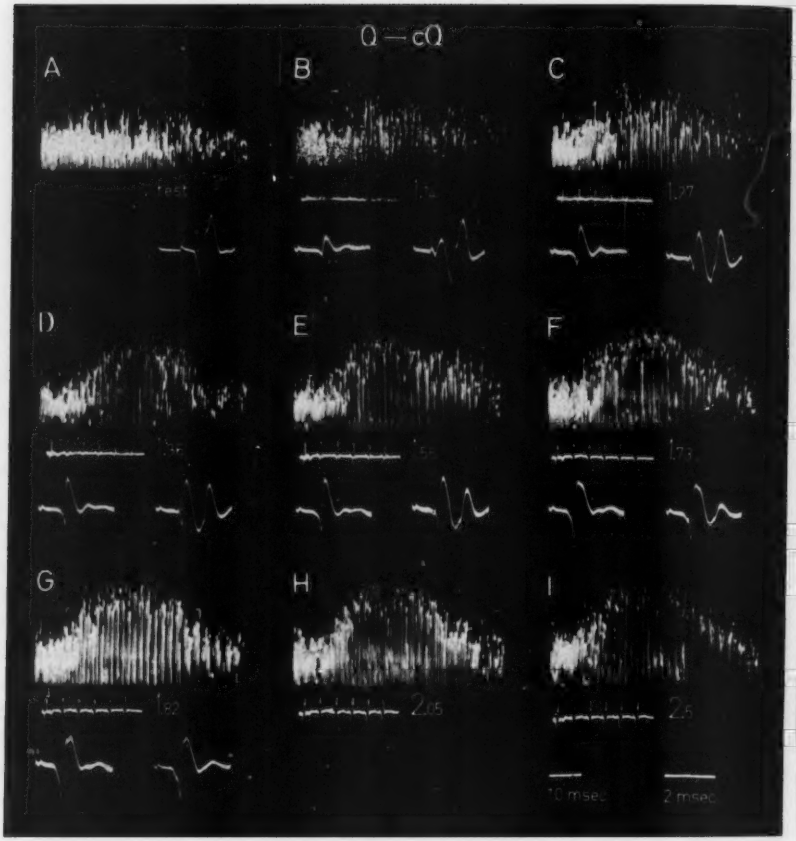

Fig. 4. Actions on the Q monosynaptic test reflexes evoked by a train of impulses in the contralateral Q nerve. Stimulus strengths expressed in multiples of threshold for the nerve are indicated. The incoming conditioning volleys were triphasically recorded in the dorsal root entry zone (middle traces) with the same time base as the test reflexes in the upper traces. Triphasic recordings at faster sweep speed of single volleys evoked at the indicated stimulus strengths are given in lower left traces and in combination with a supramaximal group I volley (shown unconditioned in A) evoked in the refractory period of the first volley in lower right traces. The records of dorsal root volleys are superimposed traces. Procedure and conventions as in Fig. 3. Chronic spinal cat.

strength was at threshold for the fibre investigated it was activated only by the first stimulus (A, E and H), only very exceptionally by any of the others (B). It is important that group II fibres in this respect closely

Fig. 5. Simultaneous recording in two dorsal root filaments. A conditioning train of 4 impulses was applied to the soleus nerve at indicated stimulus strengths expressed as multiples of the threshold for the fastest conducting fibre.

resemble group I fibres. In G at 1.7 times threshold the group II fibre (lower trace) failed to be activated in 12 trials. In H at 1.79 times threshold it responded to the first stimulus in 6 trials out of 12 (in 4 trials the fibre responded only to the first stimulus and in two trials to the first and third stimuli). In the remaining 6 trials the fibre did not respond at all. Similar findings were also made on slower conducting group II fibres. Hence no evidence was obtained suggesting subthreshold temporal summation in group II fibres at the frequencies used for conditioning in this series of experiments.

In many experiments recording was afterwards made from dorsal root filaments in order to measure the threshold of the group II fibres (cf. Fig. 6, 7 and 16). All effects appearing below threshold for group II have been accepted as group I effects, but with employment of repetitive stimulation it has often been difficult to decide whether an effect, appearing at or slightly above threshold for the group II, was evoked by impulses in high threshold group I or low threshold group II fibres. Even if the first stimulus in a train is slightly supramaximal for group I later stimuli may be submaximal, in other words, the overlap in threshold between group I and group II increases with repetitive stimulation.

Fig. 6 exemplifies crossed actions appearing at maximal group I strength but in this case it could be shown that the effect was caused by activity in group II fibres. Two stimuli (8 msec apart) to the BSt nerve were used to condition the test reflex from the contralateral BSt. In B at 1.41 times threshold the double volley test (upper right traces in each record) shows

Fig. 6. Actions of two conditioning volleys from BSt (B—D) on the contralateral BSt monosynaptic test reflexes, shown unconditioned in A. The time of arrival at the dorsal root entry zone of the conditioning BSt volleys is indicated by arrows only in the lowermost records (B and D). Triphasic recordings at faster sweep speed are shown in lower middle traces and monophasic recordings, obtained in the end of the experiment in lower right traces. The double volley test, upper middle and upper right traces, was performed as described in Fig. 4. For procedure and conventions see also Fig 5. Chronic spinal cat. Some records are retouched.

that the stimulus evoked an almost maximal group I volley but there was no crossed action. When the stimulus was raised to 1.53 times threshold, maximum group I (C) there was some facilitation, and at 1.65 times threshold, slightly supramaximal for group I, (D) the facilitation was prominent. This facilitation occurred after so short latency that its onset and early part must have been due to the first conditioning volley. Since the main increase in facilitation occurred from C to D, and since subsequent monophasic recording from a dorsal root filament revealed a trace of activity in group II fibres in C and a considerable activity in D (lower trace to the extreme right in each record of Fig. 6) it can be concluded that the facilitation in Fig. 6 was caused by impulses in group II fibres.

B. *Attempts to separate group I a and I b effects*

It is well known that among group I fibres are afferents from two receptive systems, I a fibres with annulo-spiral endings on muscle spindles and I b fibres from Golgi tendon organs. BRADLEY and ECCLES (1953) drew the attention to the fact that the group I volleys in nerves from thigh muscles often have two components and suggested that the fast component

consisted of I a fibres and the slow of I b fibres. Later investigations have corroborated this hypothesis although overlapping of the two groups has been found (LAPORTE and BESSOU 1957, ECCLES, et al. 1957). In the present context it was naturally of interest to distinguish between connections from I a and I b fibres and considerable attempts have been made to utilize the threshold separation between the slow and fast components of the group I volley. In this series of experiments the crossed actions of thigh muscles displaying this separation were studied, particularly from the Q nerve which regularly gave large crossed actions. 12 experiments were made but in some of these the separation of the two components was not marked, neither with respect to threshold nor conduction velocity.

It is, however, obvious that the employment of repetitive stimulation gives a severe limitation, because of changes in threshold with successive stimuli; the first stimulus of a train may be supraliminal for the I b component and later stimuli may not suffice to excite all fibres of the I a component.

In Fig. 4 already discussed in section A, which illustrates the action from Q to contralateral Q with graded conditioning stimulation there is a clear cut facilitation in record B where the first stimulus in the train gives a small I a volley. The facilitation increases considerably in C and D where the first volley in the train is an almost maximal I a volley, whereas there is very little sign of activation of the I b component. The surface lead recording in B—D also shows that later volleys in the train decrease markedly and represent only a fraction of the I a volley. When the stimulus strength was increased further in E—G to activate also the I b component there was only a small increase in facilitation of the contralateral Q monosynaptic reflex. This finding would suggest that the facilitation was contributed mainly by fibres of the I a component. Similarly in Fig. 15 the facilitation from Q on the contralateral DP monosynaptic reflexes appears with a very low threshold group I volley, and as in Fig. 4 it seems to be contributed by the I a component.

Although it was regularly observed that this contralateral facilitation from Q appeared at very low stimulus strengths, it was by no means always possible to ascribe it exclusively to the I a component. For example in Fig. 7 (right records in each column) and Fig. 8, both showing effects from Q to contralateral Q, it is not possible to state whether a major part of the facilitation at medium group I stimulus strength is due to activation of fibres of the I a component in the latter part of the train or to fibres of the I b component in earlier volleys.

One source of error in an attempt to interpret these actions in terms of effects by I a and I b fibres is the 'contamination' between the two groups; a small number of I b fibres may be contained in the fast component of the group I volley and, vice versa, some I a fibres in the slow component (LAPORTE and BESSOU 1957, ECCLES, et. al. 1957). This possibility is of importance since repetitive stimulation may tend to increase the effect from a small number of fibres. The findings in Fig. 7 are of interest in this respect. In this experiment the actions from Q on the contralateral monosynaptic reflexes from Q (right records in each column) were compared with the actions on the ipsilateral monosynaptic reflexes from med.G (left records in each column). In both cases a train of 4 volleys was used for conditioning and at each strength the effects were alternately recorded on both sides. At a strength of 1.15 times threshold, record C, there is contralateral facilitation and ipsilateral inhibition. These effects increase at 1.24 times threshold in D and at 1.36 times threshold in E where the double volley test indicates that the strength is maximal for the I a but subliminal or at threshold for the I b component. In F and G when the conditioning strength was raised to activate fibres of the slow component there is a considerable increase of the ipsilateral inhibition to med.G and also some augmentation in contralateral facilitation to Q. The only known connection by which group I afferents from Q ipsilaterally can inhibit the monosynaptic reflex from med.G (recorded in S_1) is by the I b pathway and the inhibition in C—E may be due to I b fibres in the fast component and, if so, impulses in these afferents might also be responsible for the crossed effects. However, the possibility still remains

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Fig. 7. The actions of a train of volleys in the Q nerve (B—G) were alternately measured on ipsilateral monosynaptic reflexes from the med.G nerve, recorded in the S_1 ventral root (left records in each column) and on contralateral monosynaptic reflexes from the Q nerve, recorded in the L_6 ventral root (right records in each column). The unconditioned test reflexes are shown in A. In the records of Q → cQ the triphasic recordings (left traces below the 'integrated' curves) show the time of arrival of the conditioning volleys; in the records of Q → i med.G the time of arrival is indicated only by arrows in the lowermost records (D and G). In B—K (lowermost left traces in B—G) the train of conditioning volleys was monophasically recorded afterwards. In E—K at faster sweep speed single volleys are also shown monophasically recorded at the given stimulus strength.

The crossed excitatory action from Q at the stimulus strengths used in E—G was sufficient to evoke reflex discharges in the L_6 ventral root, and hence also recorded at all time intervals when these motoneurones were not refractory from the test reflex. These discharges in the ventral root appear as a white shade at the base of the upper right traces in records E—G at the time of the maximal facilitatory effect on the test reflexes. Procedure and conventions as in Fig. 3, 4 and 6. Chronic spinal cat. Some records are retouched.

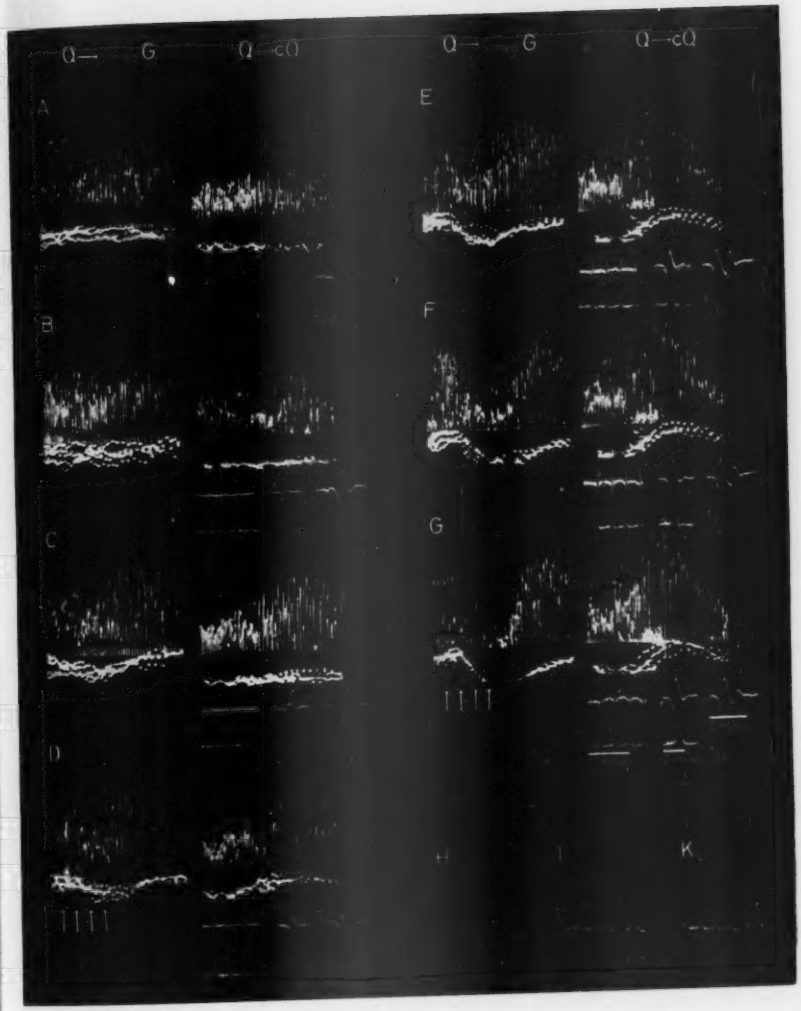

Fig. 7.

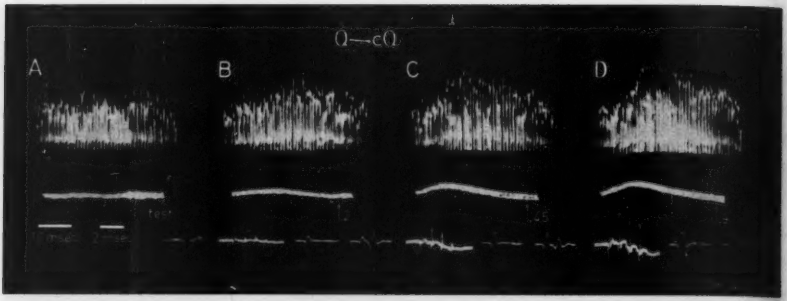

Fig. 8. Actions on the Q test reflexes evoked by volleys in the contralateral Q nerve. The same chronic spinal cat as in Fig. 9, 10, 12 and 13. Procedure and conventions as in Fig. 3 and 4.

that the actions are evoked by different fibre systems because they may have different interneuronal linkages; if the linkage of the crossed path was weaker than the ipsilateral, impulses in a larger number of afferents would be required. A more definite suggestion regarding the source of the actions evoked by impulses in low threshold muscle afferents is not permissible on the basis of the present experiments.

C. *Pattern of crossed group I actions*

Effects of repetitive stimulation of group I afferents from various thigh and leg muscles have been examined on monosynaptic reflexes from contralateral extensors and flexors. For reasons discussed in the last section, no attempt will be made to distinguish between effects by I a and I b impulses.

a) To extensors

Crossed facilitatory action between Q has already been illustrated in Fig. 4 and 7 and it will now be shown that crossed facilitatory actions are common between extensors. No inhibitory interaction was ever found between extensors. Fig. 8—10 are from the same experiment and illustrate facilitation of the Q monosynaptic reflex by short group I trains from the contralateral Q nerve (Fig. 8, B—D), from the contralateral G nerve (Fig. 9, F and G), and from the contralateral FDL nerve (Fig. 10, B and C). In this experiment facilitation of Q monosynaptic reflexes was also evoked by a train (at just maximal group I strength) from the plantaris nerve. Sometimes the effect from ankle and toe extensors to Q was quite marked at

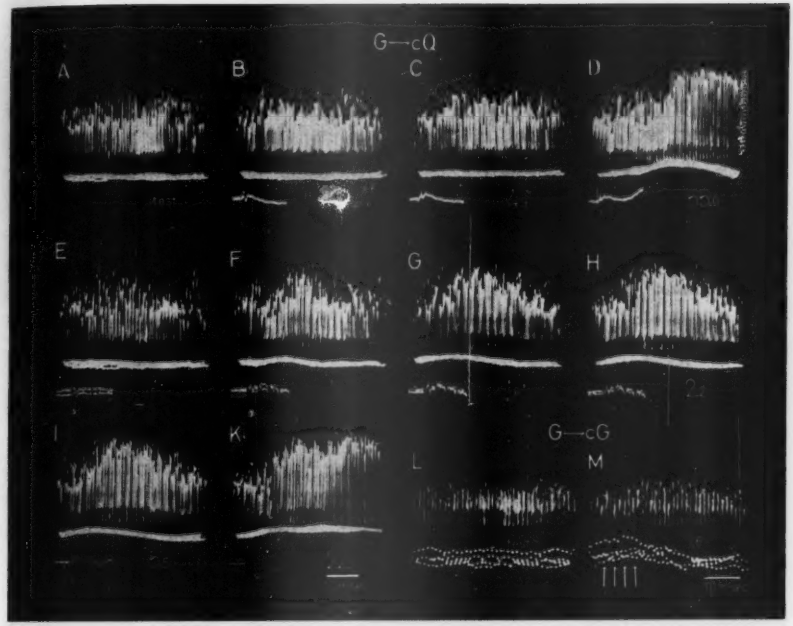

Fig. 9. Actions evoked by volleys in the G nerve on contralateral Q (B—K) and contralateral G (M) test reflexes, shown unconditioned in A and L respectively. The same chronic spinal cat as in Fig. 8, 10, 12 and 13. Procedure and conventions as in Fig. 3 and 4.

the beginning of the experiment but decreased gradually so that at the end of the experiment only the effect from Q to contralateral Q remained. In other less excitable preparations the only crossed group I action which could be obtained at all was from Q to contralateral Q.

Similar crossed facilitation of monosynaptic reflexes was also found from other extensor nerves. Record M in Fig. 9 shows the effect by a group I train in the G nerve on the contralateral G test reflexes and in this experiment the same conditioning train from G also facilitated the contralateral FDL test reflex (not illustrated). These effects from G to contralateral G and FDL were small but recorded at the end of the experiment. Crossed group I facilitation between ankle and toe extensors was not particularly prevalent, but of the same order of magnitude as that found from these muscles to the Q test reflex (cf. table 1, p. 31). On the other hand considerable facilitation has been observed from Q to contralateral G. The effects from the Q nerve were often larger and in less excitable pre-

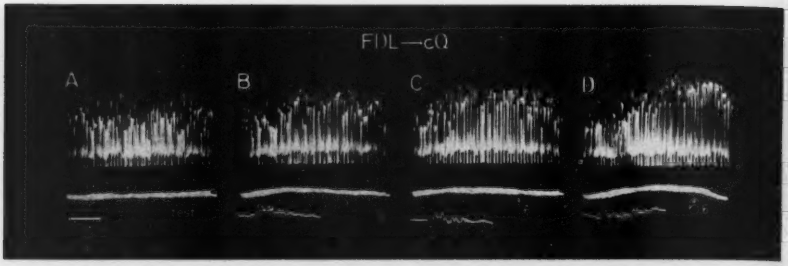

Fig. 10. Actions evoked by volleys in FDL on contralateral Q test reflexes. The same chronic spinal cat as in Fig. 8, 9, 12 and 13. Procedure and conventions as in Fig. 3 and 4.

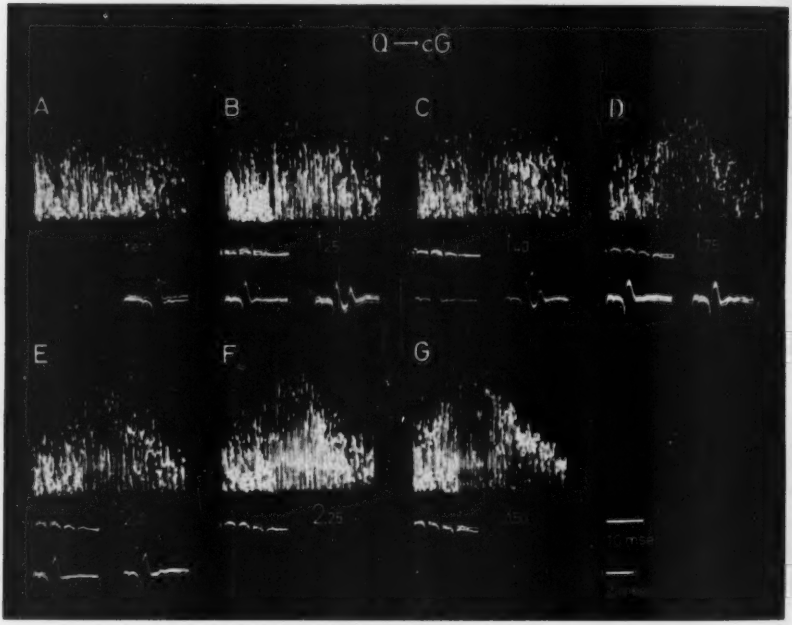

Fig. 11. Actions evoked by volleys in Q on contralateral G monosynaptic reflexes. Chronic spinal cat. Procedure and conventions as in Fig. 3 and 4. Some records are retouched.

parations this latter effect has been observed when crossed interaction between leg muscles was lacking. Fig. 11 shows the effect from Q to contralateral G. There is a weak effect in B at a strength of 1.25 times threshold and a marked increase with a more complete recruitement of group I fibres

in C—E. The triphasic recordings from the dorsal root entry zone show that the Q volley displayed separation in I a and I b components. The effect in Fig. 11 appears mainly when the slow component was included in the train. In the same experiment facilitation from Q to contralateral Q was found at a much lower stimulus strength, which activated only a small part of the fast group I component in much the same way as has been illustrated in Fig. 4. This may suggest that different afferent systems were responsible for facilitation of Q and G test reflexes; an alternative explanation could be that both effects originated from the same afferent systems but that the linkage of the former pathway was stronger and hence impulses in fewer afferents were required. In another experiment a similar comparison of the appearance of facilitation of Q and G test reflexes in relation to the size of the conditioning group I train from contralateral Q did not reveal a difference of the type described above.

To summarize: crossed facilitatory group I interaction between extensors is common and widespread (cf. table 1, p. 31). Effects from Q are more marked than from the other extensors investigated and Q is also more receptive at least with respect to effects from the contralateral Q.

There are also crossed effects by group I volleys from flexors on test reflexes from extensors. Systematic investigations have been made of crossed actions contributed from BSt and DP and important differences between the crossed group I effects on extensor test reflexes were found from these two nerves. Altogether effects from BSt were rare, but, when observed inhibitory, whereas the effects from DP were common and always facilitatory.

Fig. 12 illustrates effects from BSt to contralateral Q. In G and H at a strength submaximal to group I, a brief train of volleys inhibits the contralateral Q test reflex and the effect increases somewhat in I at a strength of 2.33 times threshold which was slightly supramaximal for group I. On further increase of the stimulus strength (L and M) this inhibition decreases and reverses to facilitation (N). The facilitatory action in L—N by impulses in high threshold afferents would be expected since single conditioning stimuli of the same strengths give this effect (D and E), whereas a single group I volley has no significant inhibitory effect, (B and C). The inhibitory group I effect from BSt is probably not limited to Q; in two cases there was probably slight group I inhibition of the contralateral G test reflex, likewise with reversal to excitation when high threshold afferents were activated. BSt provided an exception in giving opposite actions from low and from high threshold muscle afferents. Volleys in low and high threshold muscle afferents from all other nerves evoked the same modality of crossed action (cf. Fig. 9 and 13).

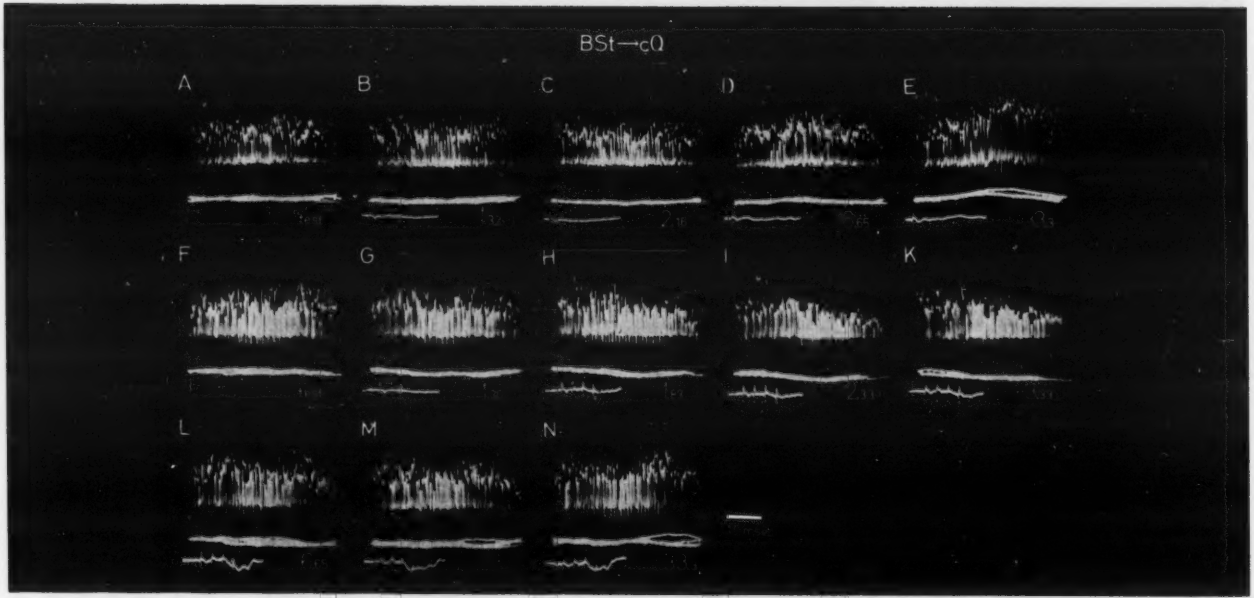

Fig. 12. Actions evoked by volleys in BSt on contralateral Q monosynaptic reflexes. The same chronic spinal cat as in Fig. 8—10 and 13. Procedure and conventions as in Fig. 3 and 4.

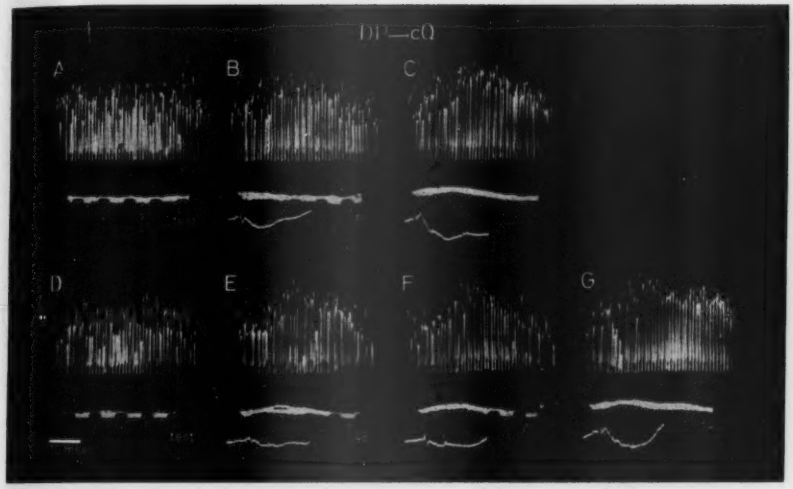

Fig. 13. Actions evoked by volleys in DP on contralateral Q monosynaptic test reflexes. The same chronic spinal cat as in Fig. 8—10 and 12. Procedure and conventions as in Fig. 3 and 4.

From DP, on the other hand, there was facilitation to contralateral Q (Fig. 13) and in contrast to the effect from BSt, this effect was found frequently. It seems likely that the effect in Fig. 13, E and F, was evoked by impulses in very low threshold group I fibres, but the detailed interpretation is somewhat complicated by the fact that the DP nerve at low stimulus strengths did not follow repetitive stimulation very well, as often happened with this nerve (cf. triphasic recordings in Fig. 13, 14 and 17). Group I volleys from DP have also been observed to facilitate contralateral G but this effect was much smaller than to contralateral Q.

Both from BSt and DP the largest crossed group I actions were found on the Q test reflex. It should, however, be remembered that Q is not a uniform muscle. V-Cr (vasto-crureus) is a pure knee extensor but R (rectus), being a double joint muscle, can in addition act as a hip flexor. The crossed effect from DP is presumably associated with the extensor function because, when monosynaptic reflexes from R and V-Cr were investigated separately, both were facilitated in much the same way as is illustrated in Fig. 14 (with four different strengths of DP stimulation). In the same experiment it was also found that a conditioning group I train from the Q nerve facilitated contralateral R and V-Cr reflexes in parallel as in Fig. 14.

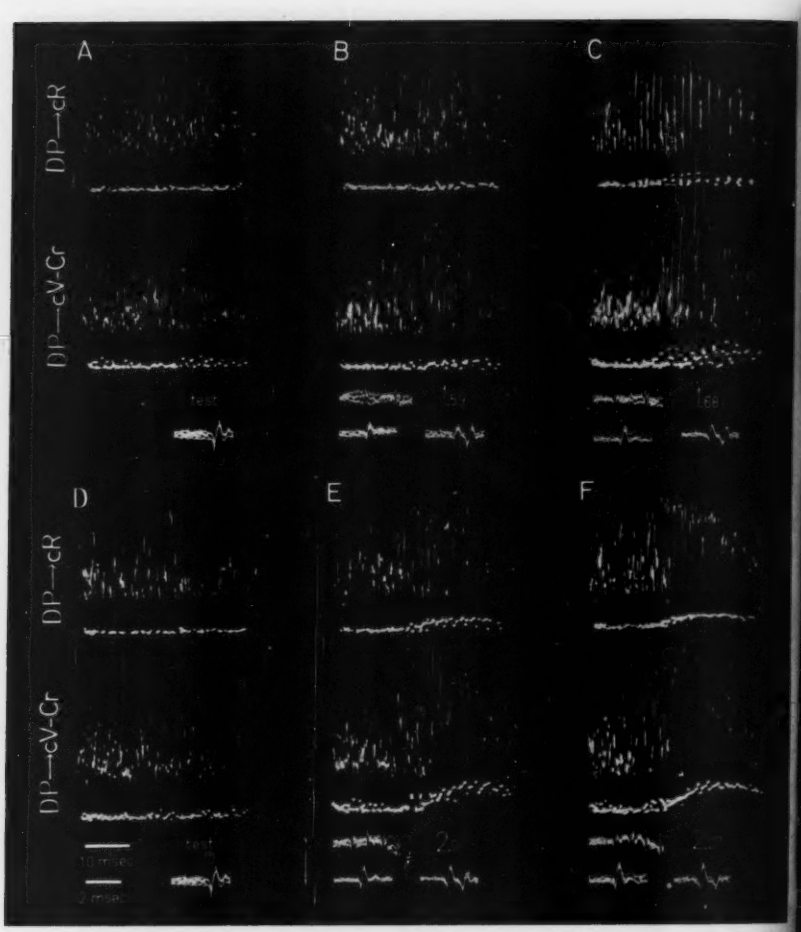

Fig. 14. Crossed effects evoked by volleys in the DP nerve on monosynaptic reflexes from R and V-Cr as indicated. At each conditioning strength alternate recording was made of the effect on both test reflexes. Chronic spinal cat. Procedure and conventions as in Fig. 3 and 4. Some records are retouched.

Fig. 15. Actions on DP monosynaptic reflexes evoked by volleys in the contralateral Q nerve. Chronic spinal cat. Procedure and conventions as in Fig. 3 and 4.

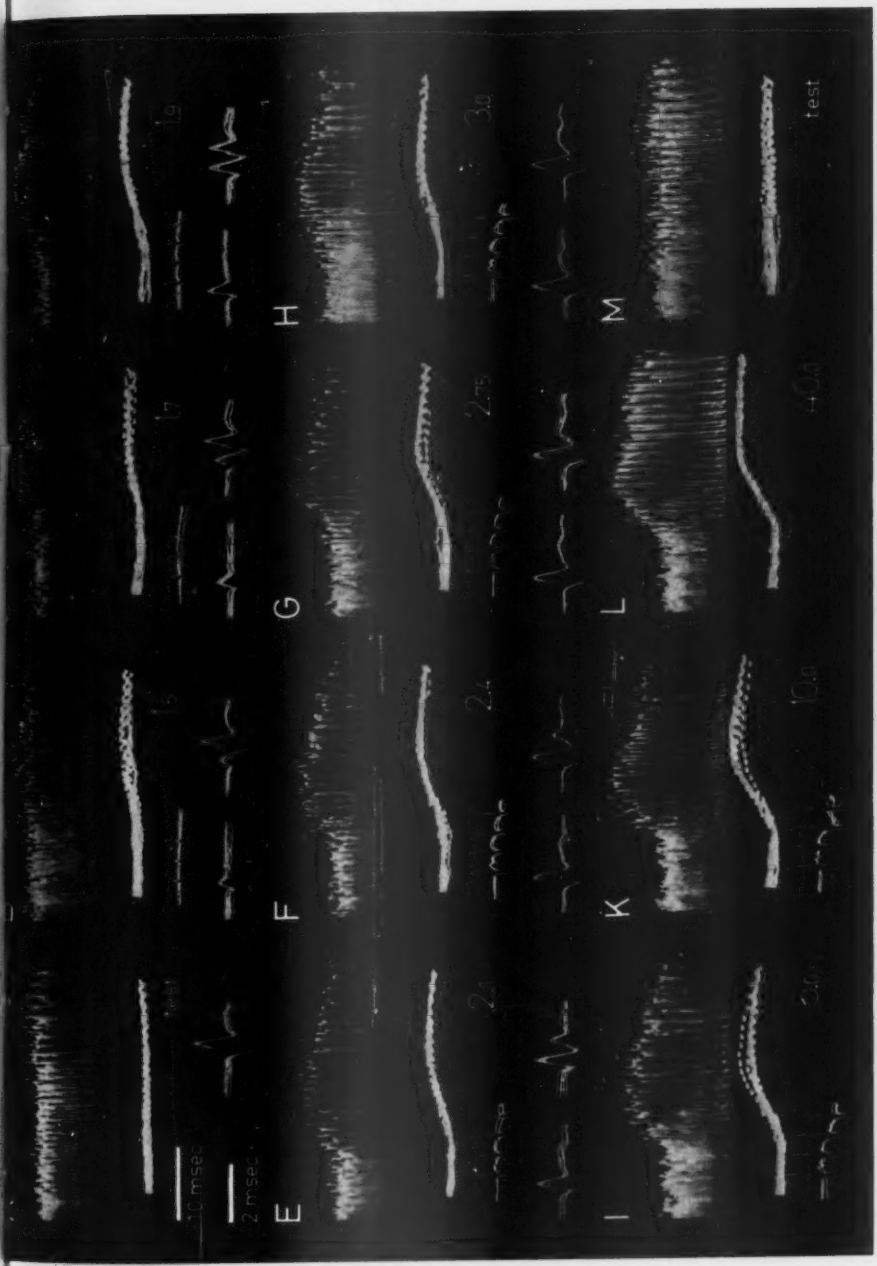

Fig. 15.

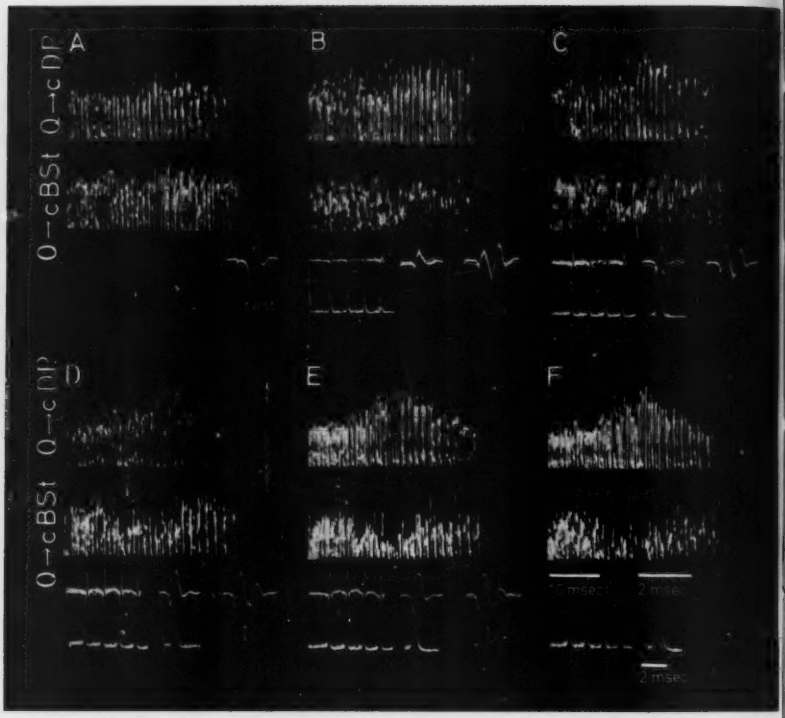

Fig. 16. Effects by volleys in the Q nerve on the contralateral DP test reflexes and on the contralateral BSt monosynaptic test reflexes, as indicated. At each conditioning strength alternate recording was made. Chronic spinal cat. Procedure and conventions as in Fig. 3, 4, 6 and 7.

b) To flexors

Systematic investigations were made only of the effects on BSt and DP monosynaptic reflexes. The most marked effects were found from the Q nerve. Fig. 15 shows the frequently occurring crossed facilitation from Q to contralateral DP. As has already been discussed in section B the effect appears with small group I volleys in B and C and does not increase significantly when slower conducting group I fibres are included in the conditioning train (F—H).

Test reflexes from BSt, on the other hand, were inhibited by a group I train from the contralateral Q nerve. This is illustrated in Fig. 16 where at each conditioning strength this inhibitory effect is compared with the

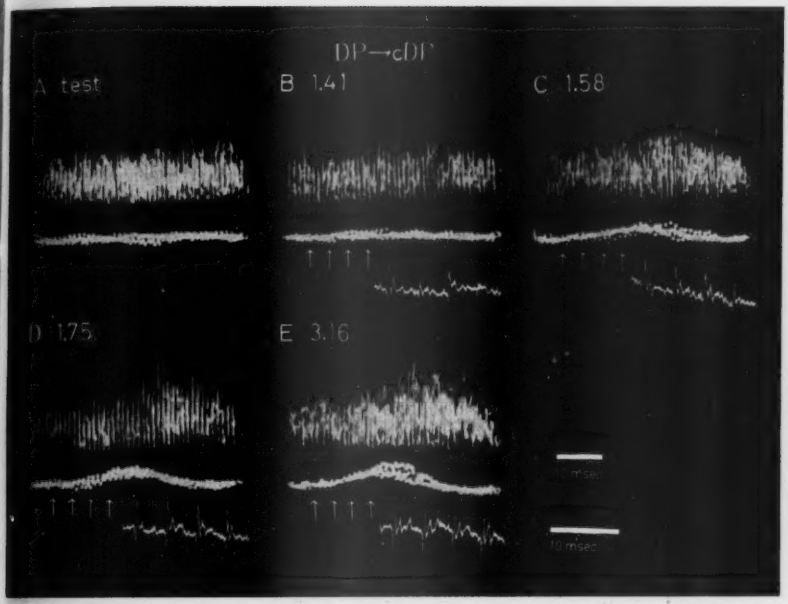

Fig. 17. Actions evoked by volleys in the DP nerve on the contralateral DP monosynaptic reflexes. The train of conditioning volleys was triphasically recorded at the dorsal root entry zone but at faster sweep speed (lowermost traces). Otherwise the procedure and conventions were as in Fig. 3. Chronic spinal cat.

facilitation of the contralateral DP reflexes. Both effects appear in B at a strength of 1.24 times threshold and the differences in growth between the two crossed actions with increasing strength (C—E) is not sufficiently marked to justify a suggestion that different receptive systems were responsible. The question may be raised whether the difference in modality of action can be related to the fact that Q is the contralateral antagonist of BSt whereas DP operates at another joint. No evidence in this direction is given by the group I actions to DP from the crossed antagonist FDL. A short train from this nerve, evoked at maximal group I strength, produced facilitation probably due to activity in group I fibres.

Of crossed connections between flexors, the only more frequent effect was facilitation to DP by a maximal group I train from contralateral DP, which effect presumably could be ascribed to group I afferents. This is illustrated in Fig. 17. There is probably no effect in B at 1.41 times threshold, but a marked effect in C at 1.58 and in D at 1.75 times threshold, which was just maximal for group I. The increment in effect is probably

mainly due to the more effective activation of later volleys in the train (cf. triphasic recordings, lower traces). From BSt to contralateral BSt there were never any effects which could be ascribed to impulses in group I afferents (cf. Fig. 6).

A train of group I volleys, particularly in the Q nerve, sometimes evoked a discharge in contralateral motoneurones (Fig. 7). It was, however, controlled that all the actions described in this chapter were not secondary effects to a crossed reflex discharge (cf. RENSHAW 1941, ECCLES et al. 1954, WILSON 1959, WILSON, TALBOT and DIECKE 1960), since they were also found when there was no sign of crossed reflex discharges.

Table 1.
Actions evoked by a train of conditioning group I volleys on contralateral test reflexes.

Contralateral test reflex	Conditioning nerve					
	Q	G	Pl	FDL	BSt	DP
Q	+	+	+	+	−	+
G	+	+		(+)	(−)	(+)
FDL	+	+		(+)		
BSt	−					
DP	+			(+)		(+)

Table 1 summarizes the crossed actions evoked by a train of impulses which could be ascribed to group I afferents. + denotes facilitation of the contralateral test reflex and — inhibition. Actions within brackets indicate effects which either were weak or evoked at just maximal group I strength without further analyses to ascertain the origin of the effects ascribed above. Even fine gradation of conditioning stimulus strength never revealed any signs of dual actions by impulses in group I afferents.

Discussion

In the present investigation on acute low spinal cats no crossed group I effects on contralateral monosynaptic test reflexes were discernable on single or repetitive stimulation. Even in chronic spinal animals single conditioning group I volleys gave no or only small effects whereas a brief train of stimuli produced considerable crossed actions. Repetitive stimulation provides a complication but the criteria for ascribing effects to group I afferents have been given in section A.

Any relevant discussion of the functional organization of group I connections must consider the I a and I b systems separately. In many experiments of this series attempts were made to utilize the two components of

the group I volley to disclose I a and I b effects (cf. BRADLEY and ECCLES 1953, ECCLES, et al. 1957, LAPORTE and BESSOU 1957). The employment of repetitive stimulation undoubtedly complicates the interpretation because it gives a threshold overlap between the fast and the slow component (cf. section A). Furthermore it has recently been shown that some synaptic actions of I b impulses are considerably enhanced when repetitive stimulation is employed, while synaptic actions from I a fibres are decreased (CURTIS and ECCLES 1960, ECCLES, HUBBARD and OSCARSSON 1961). Nevertheless it seemed worth while to try this technique. The results were puzzling; facilitation from Q to contralateral Q appeared with stimulation of low threshold group I fibres (cf. Fig. 4) and did not always increase when the I b component was included. In other experiments the I b component probably also contributed facilitation. This finding may indicate that crossed I a facilitation from Q to contralateral Q can occur but at present it cannot be excluded that the facilitatory effect of the I a volley is due to 'contamination' of I b fibres in this component (cf. control experiment in Fig. 7).

Crossed effects which could be ascribed to impulses in group I afferents are summarized in table 1. Facilitatory interaction between extensors was common. The most marked effects were observed from the Q nerve and reached not only contralateral Q but also all other extensors tested. In no case were dual crossed actions by impulses in group I afferents observed.

The crossed group I facilitatory effect from extensors to extensor test reflexes was not regularly reciprocated by crossed inhibition from flexors, but inhibition from BSt to contralateral Q has been observed. Group I trains from the DP nerve, on the other hand, regularly facilitated the contralateral Q test reflex. In their receptiveness BSt and DP also displayed characteristic differences (cf. table 1). DP test reflexes were frequently group I facilitated from the contralateral Q nerve, whereas BSt test reflexes were inhibited. These findings suggest that there are important differences in crossed connections to knee and ankle flexors. It is not known whether these differences have any relation to the fact that tibialis anterior has two components with different contraction time (GORDON and PHILLIPS 1953).

There are several discrepancies between the present results and those reported by PERL (1958). In the present series of experiments fine gradation of stimulus strength did not reveal dual crossed group I actions. PERL (1958), on the other hand, described a weak short lasting (3 msec) inhibition to contralateral V-Cr by a single small group I volley from V-Cr followed by a prominent long lasting (10 msec) facilitation when a larger group I volley was used for conditioning. To the nucleus of the

antagonist (BSt) PERL found, though less regularly, a reciprocal set of actions. These actions were assumed to be I a and I b effects respectively. If so, repetitive conditioning volleys at frequencies employed in this investigation would, for two reasons, favour the appearance of these latter actions, partly because of the above mentioned difference in synaptic transmittability of I a and I b impulses (CURTIS and ECCLES 1960, ECCLES et al. 1961), and partly because of the difference in duration and magnitude of the inhibitory and facilitatory actions described by PERL. PERL (1958) also claimed two sets of crossed reciprocal group I actions from BSt. Of these four effects, the only one found by repetitive stimulation was the inhibition from BSt to contralateral Q.

It is of interest to correlate these findings with previous experiments on reflex contractions in muscles. The most prominent crossed spinal reflex between knee extensors is Philippson's reflex, which is the crossed correlate to the ipsilateral lengthening reaction (SHERRINGTON 1909 a). It is generally assumed that the lengthening reaction is a I b effect (cf. GRANIT 1955) and it has also been suggested that Philippson's reflex is caused by impulses in I b fibres (MOUNTCASTLE 1956, PERL 1958). In SHERRINGTON's experiments there was usually relaxation of the contralateral Q during the shortening reaction, which is generally accepted as a I a effect, but there was sometimes contration of the contralateral Q. The possibility must, however, be kept in mind that these effects may be due to other receptive systems, possibly co-activated with I a when Q was stretched.

It is important to keep in mind that Q is a composite muscle and that fractions of it may receive different crossed connections (cf. ECCLES and GRANIT 1929). However, in the present investigation the effect of conditioning volleys from Q and DP on contralateral test reflexes from R and V-Cr closely resembled each other. Another possibility has not been excluded; crossed connections to the vastii and crureus may be different, the former muscles being engaged in phasic movements and the latter in posture where a crossed I a excitation from Q to crureus could be purposeful in standing. Furthermore there is also the possibility that on the conditioning side the various fractions of Q may have different connections to one and the same contralateral nucleus.

Summary

Crossed effects of volleys in group I muscle afferents on monosynaptic test reflexes have been investigated in unanaesthetized cats. In acute low spinal cats single group I volleys or a train of group I volleys had no effect.

In chronic spinal cats single group I volleys gave only small effects but a train of volleys gave large effects. The criteria for ascribing these effects to group I afferents have been given in section A.

Attempts to utilize the fast and slow components of the group I volleys to distinguish between effects evoked by impulses in I a and I b fibres were not successful (section B). Experiments with fine gradations of stimulus strength did not give evidence of dual crossed group I effects.

The pattern of crossed group I effects is described in section C and summarized in table 1. Crossed facilitatory interaction between extensors was common; particularly large effects were evoked from and received by Q. Crossed effects were also found from flexors to extensors; there was facilitation from DP to Q and occasionally inhibition from BSt to Q.

Of crossed group I effects to flexors the most marked were facilitation from Q to DP and inhibition from Q to BSt.

Chapter III

Crossed spinal actions from the flexor reflex afferents

Introduction

Group II and III muscle afferents, high threshold joint afferents and skin afferents have been denoted the flexor reflex afferents (FRA) (ECCLES and LUNDBERG 1959 a, HOLMQVIST, LUNDBERG and OSCARSSON 1960), because in spinal preparations they evoke prominent ipsilateral actions in motoneurones in conformity with the flexion reflex (SHERRINGTON 1910), namely excitation of flexor and inhibition of extensor motor nuclei (cf. also LLOYD 1943, BROCK, ECCLES and RALL 1951, LAPORTE and LLOYD 1952, ECCLES and LUNDBERG 1959 a).

The question now arises whether these afferent fibre systems also evoke crossed actions in accordance with the crossed extensor reflex appearing concomitantly with the ipsilateral flexion reflex. According to SHERRINGTON (1909 a, 1910), nociceptive stimulation as well as electrical stimulation of skin and muscle nerves, giving an ipsilateral flexion reflex, can evoke a movement of the fellow hindlimb with extension of the hip, knee and ankle. The muscles contracting in the crossed extension reflex were those relaxing in the ipsilateral flexion reflex, i.e. the extensors. Other muscles which relaxed in the crossed extensor reflex were those contracting in the ipsilateral flexor reflex, i.e. the flexors. The threshold for these crossed actions were sometimes about the same as for the ipsilateral reflex but occasionally considerably higher (cf. also MC COUCH, SNAPE and STEWART 1935). The latency of the crossed action (40—100 msec) was invariably longer than that of the ipsilateral reflex (8—10 msec) and sometimes considerably delayed. In addition the contralateral reflex was characterized by a gradual onset and development (LIDDELL and SHERRINGTON 1923 a, b, CREED et al. 1932).

An investigation with the aim to correlate various crossed actions to certain muscle afferent fibre systems has been made by PERL (1958). He found a complex pattern of actions from high threshold muscle afferents: the BSt monosynaptic test reflex was inhibited by a group II volley applied to the contralateral BSt, but the action reversed when thinner fibres were included in the conditioning volley. The most prominent action to the

V-Cr and G test reflexes was a longlasting facilitation evoked by activity in the thinnest myelinated fibres of flexors as well as extensors of the knee and ankle. PERL (1957) also described two sets of double reciprocal action by impulses in cutaneous nerves. A volley involving only coarse (14—6 μ) fibres resulted in excitation (central delay 3 msec) of the contralateral flexors at the knee and ankle and inhibition of extensors whereas activity in thinner cutaneous fibres (6—2 μ) gave a late (central delay 6—30 msec) prolonged inhibition to contralateral flexors and a corresponding late facilitation to contralateral extensors.

This chapter deals with the crossed effects by impulses in the FRA in acute spinal and in chronic low spinal cats.

Results

A. *High threshold muscle afferents*

In the previous chapter the attention was drawn to the fact that in chronic spinal cats a single volley usually did not evoke any crossed effects as long as only group I fibres were activated but when the stimulus strength was raised to activate thinner fibres crossed effects appeared (cf. Fig. 9, 12 and 13). Similar findings were also made in acute spinal animals. The main investigation on crossed actions from high threshold afferents was performed on acute spinal animals and findings on chronic spinal animals will be summarized at the end of this chapter. It could be excluded that the actions to be described were secondary effects to crossed reflex discharges (RENSHAW 1941, ECCLES et al. 1954, WILSON 1959, WILSON et al. 1960).

No essential difference was noted between crossed actions in animals with the cord transected in Th_{12}—L_2 and those with a medial lesion at obex (cf. table 2 A, p. 41; figures within brackets represent the number of experiments with lesion at obex). A comparison has also been made of the crossed actions found after a lesion at obex and after subsequent transection of the cord in the upper lumbar region, and it was found that the latter section did not alter the results. For this reason the results obtained in these two types of preparations have been treated as a unity.

Fig. 18 illustrates the crossed effect of a conditioning volley from the Q nerve on the DP test reflexes. In B at 1.65 times threshold, which was maximal for group I, there was no effect (unconditioned test reflexes shown in A). In D at a strength of 4.7 times threshold there appeared a clear cut facilitation which increased in E, F and G at 8.5, 11 and 30 times threshold respectively. According to ECCLES and LUNDBERG (1959 a), group II fibres can be recruited up to 8—10 times threshold while group III fibres are

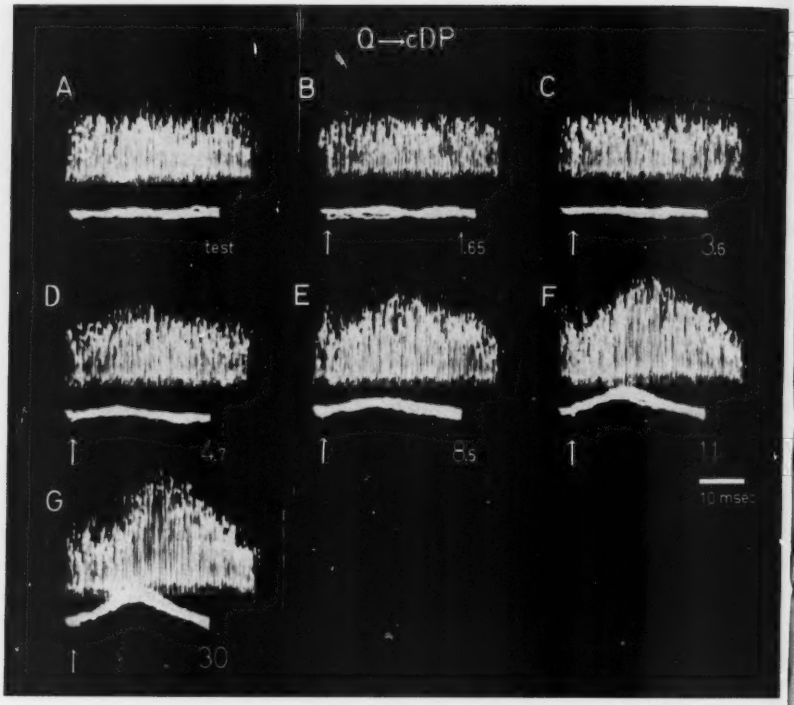

Fig. 18. Actions evoked by volleys in the Q nerve on the contralateral DP monosynaptic test reflexes. Acute spinal (L_3) cat, the same as in Fig. 19. Procedure and conventions as in Fig. 3.

activated at higher stimulus strengths, hence the effect in D can be ascribed to group II afferents and the increase in facilitation from E and F to G to impulses in group III fibres. It is of special importance that also group II volleys from the G nerve have been found to give significant crossed actions (cf. Fig. 20 A and 21 F), because the quantitative identification of group II fibres as spindle afferents (HUNT 1954) was made on gastrocnemius-soleus afferents. There was usually as in Fig. 18 an increase of crossed actions when the stimulus strength was raised from a value activating most of the group II fibres to one activating group III fibres. However, sometimes a group II volley did not give any detectable crossed actions. In such cases group III volleys usually contributed large effects. On the other hand, in preparations with pronounced crossed actions by group II fibres, evoked at a conditioning strength of 5 times threshold, there

was only a small augmentation of the crossed facilitation when the conditioning volley was raised to include fibres in the group III range (cf. Fig. 20 B, D and F). In no case did low threshold group II volleys and group III volleys evoke actions of opposite modality (i.e. excitation or inhibition).

The method employed for recording in Fig. 18 is less suitable for latency measurements. In this respect the technique to record the effect at fixed intervals is preferable. In excitable preparations there are often inhibitory or excitatory actions, when the group I component of the conditioning volley preceded the testing by 5 msec at the dorsal root entry zone. Subtracting 1—2 msec for slower conduction velocity leaves about 3—4 msec for the central transmission. Intracellular recordings have been made of crossed actions from high threshold muscle afferents and in these experiments the minimal central latency for EPSPs was 3.5 msec (HOLMQVIST and LUNDBERG, unpublished). These delays suggest transmission through several interneurones. However, this central delay was often some msec longer. The duration of crossed actions varied with the condition of the preparation and the stimulus strength used, but the action often lasted about 25 msec. This initial effect was sometimes followed by a prolonged reversed action, which was not systematically analysed.

High threshold muscle afferents from various muscles evoke in the same contralateral motor nucleus very similar actions, a feature also found for their actions on ipsilateral motor nuclei (ECCLES and LUNDBERG 1959 a). Fig. 19 is from the same experiment as Fig. 18 and shows that single volleys in high threshold afferents from flexors (B and C) evoke a facilitation of the contralateral DP resembling the one evoked from Q (Fig. 18) and from other extensors (Fig. 19 D—F). In 22 experiments there were only two exceptions to this rule, in both cases volleys in high threshold afferents from Q gave different crossed actions than corresponding volleys from other muscle nerves.

The different extensor nuclei investigated (Q, G, Pl and FDL) almost invariably received the same modality of crossed action from the high threshold muscle afferents. The only crossed flexor nucleus regularly investigated was BSt, but when DP occasionally was tested its receptiveness was found to coincide with that of BSt (cf. table 2 A, p. 41). It should, however, be observed that the receptiveness of DP was never investigated in an experiment in which BSt was inhibited from high threshold muscle afferents.

In spinal cats in good condition volleys in the FRA usually excite flexor nuclei and inhibit extensor nuclei on the ipsilateral side (ECCLES and

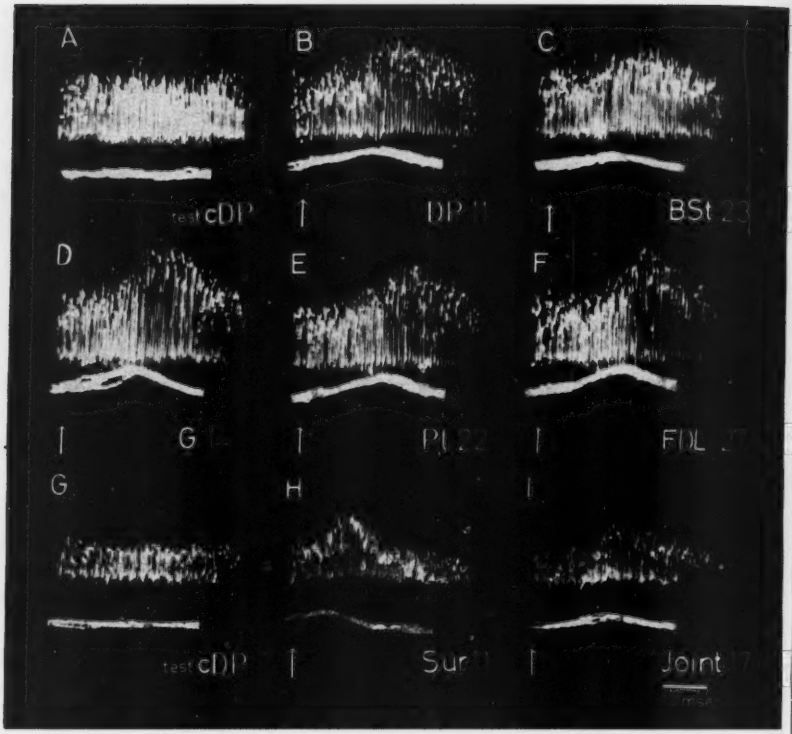

Fig. 19. Crossed actions on DP monosynaptic test reflexes, shown unconditioned in A and G, evoked by volleys in the various nerves indicated. Records G—I were taken with lower amplification than records A—F. The same acute spinal (L_2) cat as in Fig. 18. Procedure and conventions as in Fig. 3.

LUNDBERG 1959 a). Crossed actions from the FRA in accordance with the scheme of double reciprocal innervation, i.e. excitation to extensor and inhibition to flexor nuclei, has also been observed. This is exemplified by the experiment illustrated in Fig. 20, in which volleys in high threshold muscle afferents gave excitation to the contralateral extensor nuclei G (curves in A—C) and Pl (curves in D), while the contralateral flexor nucleus BSt received inhibition (curves in E—G).

The pattern of crossed actions from high threshold muscle afferents was by no means as constant (table 2 A) as the pattern of their ipsilateral effects. Thus, reverse crossed actions to the ones described above have also been found. This is illustrated in Fig. 21 A and B. In this experiment

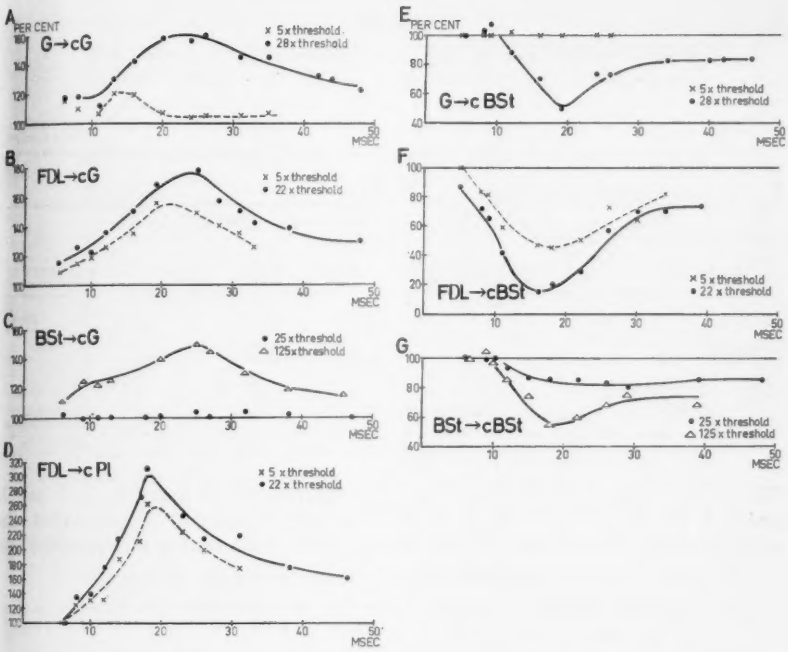

Fig. 20. Curves of crossed actions on G (A—C), Pl (D) and BSt (E—G) monosynaptic test reflexes evoked by conditioning volleys in the nerves to G (A and E), FDL (B, D and F) and BSt (C and G) at stimulus strengths given. Comparatively high stimulus strengths for conditioning were required to evoke effects from the BSt nerve (C and G) but an abnormally high strength was also necessary to obtain a maximal group I volley probably because of damage to the nerve. Acute spinal (L_2) cat. Procedure and conventions as in Fig. 1.

the contralateral flexors were facilitated and the contralateral extensors inhibited. Apparently impulses in high threshold muscle afferents can excite as well as inhibit the same contralateral motor nuclei. Of considerable interest is the findings that group II and III volleys do not always reciprocally influence the crossed extensors and flexors. This is shown by the two other experiments in Fig. 21, one illustrated in C and D, and the other in E and F. High threshold muscle afferents in one preparation inhibited the extensor G (C) as well as the flexor BSt (D), while in the other preparation both the extensor and the flexor were facilitated (E and F). A further survey of the crossed actions in these three situations will be found in the spinal pattern of Fig. 30, 31 and 25—29 respectively. It is noteworthy that also at a conditioning strength of 5 times threshold,

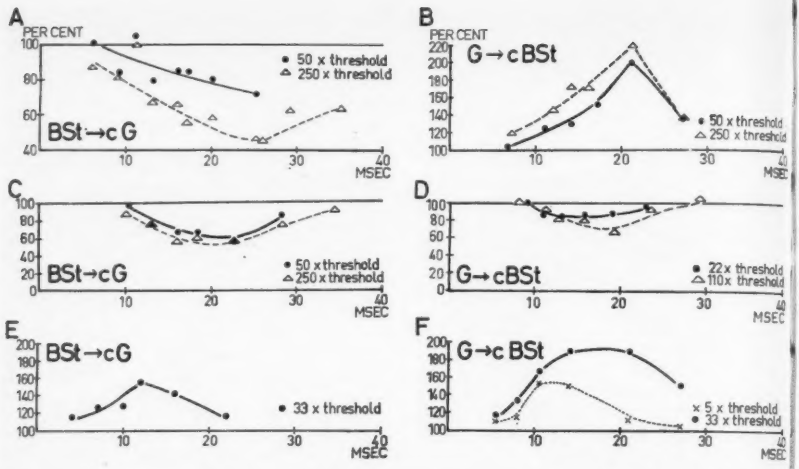

Fig. 21. The curves were obtained from three experiments: 1) A and B, 2) C and D and 3) E and F. The curves in A—D were from cats with lesions at obex, while the curves in E and F were from a cat with acute section of the cord in L_2. Procedure and conventions as in Fig. 1 and 20.

actions of opposite modality on the same contralateral nucleus have been found in different preparations.

There were also other indications of variability in the crossed actions from the FRA. In some preparations there were poor actions to one type of motor nuclei of synergic muscles (extensors or flexors) during the whole course of the experiment, while there were prominent actions to motor nuclei of their antagonists. For instance, though there was marked crossed facilitation to DP in Fig. 18 and 19 and also to BSt, there were scarcely any crossed effects to the extensors, Q, G and Pl in this experiment. In other experiments pronounced crossed actions developed during the course of the experiment. For example, this was the case in the experiment illustrated in Fig. 25—28. There the facilitation to the flexors DP (Fig. 27) and BSt (Fig. 28) could be disclosed very soon after spinal transection and remained fairly unchanged during the following hours, whereas facilitation to the extensor nuclei Q (Fig. 25), G (Fig. 26), and FDL (not illustrated) did not appear until some hours after the transection. When crossed actions from high threshold muscle afferents had once been established they generally remained, but marked fluctuations or changes have been observed. In some experiments pronounced crossed actions to motor nuclei of synergic muscles disappeared, while those to the nuclei of the antagonists did not alter. In

Table 2 A.

The pattern of crossed actions from high threshold muscle afferents in 'acute spinal cats'. Figures within brackets indicate the number of animals with a medial lesion at obex. In the remaining animals the cord was transected in Th_{12}—L_2.

Action to extensor nuclei	Action to BSt	Number of experiments
+	+	7[1] (4)
+	−	3
−	+	3[2] (1)
−	−	2 (1)
+	0	1
0	+	4
0	−	2 (1)
		22 (7)

[1] In 2 cases also excitation to DP.
[2] In 1 case also excitation to DP.

Table 2 B.

The pattern of crossed actions from high threshold muscle afferents in 'chronic spinal cats'. In these animals the cord had been transected in L_1—L_2, 2—6 weeks before the experiments. Figures within brackets indicate the number of experiments on animals without laminectomy (cf. methods).

Action to extensor nuclei	Action to BSt	Action to DP	Number of experiments
+	+	+	2
+	+		5 (3)
+	0	+	1
+	0		1
+	−	+	4
+	−		3 (1)
			16 (4)

one case there was even a reversal of crossed effects to BSt with a change from inhibition to excitation during the course of the experiment, and in another experiment there was initially a crossed pattern of actions in conformity with the crossed extension reflex, but after a short interval the modality of crossed actions reversed to both G and BSt and remained so until the cat died one hour later.

Table 2 A summarizes the findings in acute spinal cats. As mentioned above all four possibilities of variations of crossed actions to extensors and flexors (BSt) have been found, but the table shows that the two types with

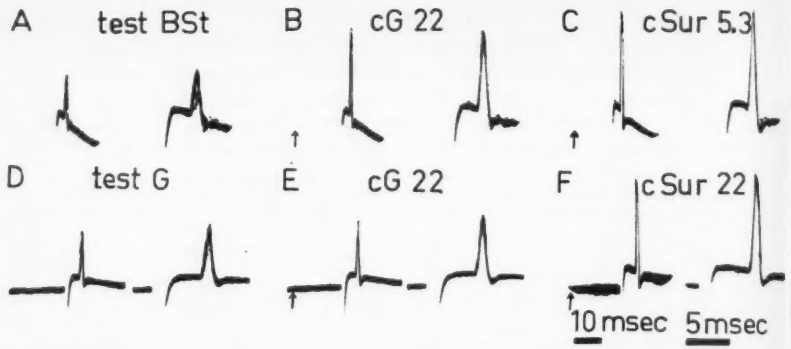

Fig. 22. Monosynaptic reflexes evoked and recorded in the peripheral nerve to BSt (A—C) and G (D—F). Conditioning stimuli were applied to the contralateral G nerve (B and E) and sural nerve (C and F) at times indicated by the arrows. Chronic spinal cat. Procedure and conventions as in Fig. 2. Some records are retouched.

excitation to extensors dominated and the combination with facilitation to flexors was most common. The frequent occurrence of these two combinations in acute spinal cats is of interest because in chronic spinal animals only these two types of patterns were met with (table 2 B).

The common absence of reciprocity of crossed actions by volleys in high threshold muscle afferents was a surprising finding, specially in chronic spinal animals, and it may be questioned whether this is an artefact caused by the extensive dissection. In order to reduce the trauma to a minimum, four experiments were made on chronic cats not subjected to laminectomy. The monosynaptic reflex discharges were evoked and recorded peripherally from the muscle nerves as described under methods. In three of these experiments test reflexes to flexors as well as extensors were facilitated (Fig. 22) while facilitation of extensors linked with inhibition of BSt test reflexes was found only in one case (cf. figures within brackets in table 2 B).

On four occasions it was observed in chronic spinal cats that the synergic motor nuclei DP and BSt received opposite actions (cf. table 2 B). The former was facilitated, whereas the latter was inhibited. Similar differences (but in opposite direction) have also been found for their ipsilateral receptiveness (Eccles and Lundberg 1959 a, Paintal 1961, Holmqvist and Lundberg 1961).

In chronic spinal cats the threshold for crossed actions was often low, and quite prominent crossed actions could often be evoked at conditioning stimulus strengths slightly supramaximal for group I (cf. Fig. 6).

B. *Skin afferents and high threshold joint afferents*

Impulses in skin and high threshold joint afferents evoke ipsilateral actions resembling those evoked from high threshold muscle afferents. This is also true with respect to their crossed actions as exemplified in Fig. 19 H and I. With only a few exceptions it has been found that impulses in skin and joint afferents produce the same modality of actions as impulses in high threshold muscle afferents.

Experiments with graded stimulation revealed that no crossed actions from joint afferents could be recorded until the stimulus strength was raised to about 2.5 times threshold for the nerve. For these experiments the volley evoked by stimulation of the knee joint nerve was recorded triphasically from the sciatic nerve and the threshold of the nerve could be measured accurately. Hence it can be concluded that impulses in the coarse joint afferents do not give rise to any actions in contralateral motoneurones, a phenomenon already described for other systems activated by the FRA (OSCARSSON 1957, 1958, ECCLES and LUNDBERG 1959 a). Fig. 23 shows the effect to the contralateral G monosynaptic test reflex, peripherally recorded at increasing strength of stimulation of the posterior knee joint nerve. In this experiment the stimulus strengths are expressed in multiples of the threshold for the minimal detectable dorsal horn potential. This potential is presumably due to interneuronal activity caused by impulses in joint afferents and cannot be obtained until the stimulus strength is raised above 2 times threshold for the joint nerve. Thus the appearance of the facilitatory action at 1.5 times threshold for the dorsal horn potential in A means a stimulus strength > 3 times threshold for the nerve. With only a slight rise in stimulus strength the effect increases to a maximal value as shown in C at 3 times threshold for the dorsal horn potential (> 6 times threshold for the nerve). A further increase in the stimulus strength only gives a slight prolongation of the effect as is shown in D at 40 times threshold for the dorsal horn potential (> 80 times threshold for the nerve). The latency for the action has been estimated to 5 msec, assuming that the fastest conducting fibres, which give effect, have a diameter less than 8 μ. Sometimes there was a longer central delay for actions evoked by high threshold joint afferents.

The curves in Fig. 23 were obtained from a chronic spinal cat. In these preparations it was observed that the crossed facilitatory actions from the joint nerve were extremely powerful and could often evoke a more prominent effect than a single volley in a muscle or skin nerve. Unfortunately, the posterior nerve to the knee joint was not dissected in any of the chronic spinal animals with crossed inhibitory actions to BSt, thus

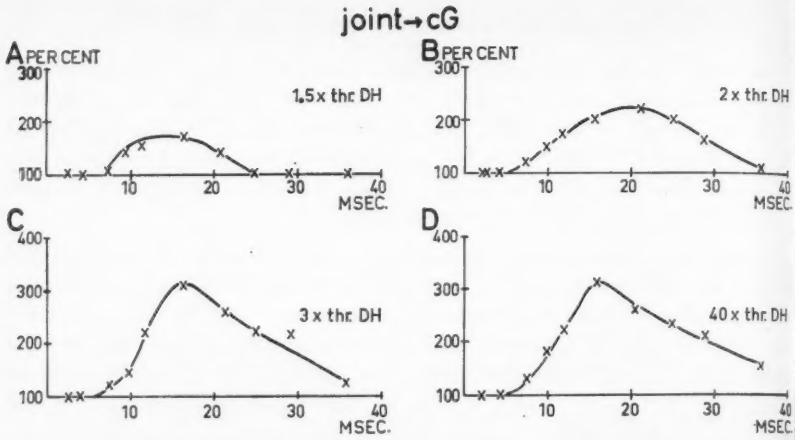

Fig. 23. Crossed actions on G monosynaptic reflexes evoked by single conditioning volleys in the posterior knee joint nerve at stimulus strengths expressed in multiples of the minimal observable dorsal horn potential. The test reflexes were recorded peripherally (as in Fig. 22). The intervals between conditioning and testing stimuli are given on the abscissa. Chronic spinal cat. Procedure and conventions as in Fig. 1.

it was not possible to test whether the inhibitory pathways from the joint afferents were equally potent.

Crossed effects from the joint nerve were investigated in 9 experiments (7 acute and 2 chronic spinal cats). In 8 experiments these volleys evoked the same actions as high threshold muscle afferents (cf. Fig. 19, 29 and 31).

Cutaneous nerves consist of heterogeneous afferent fibre systems which by adequate activation are known to evoke complex actions to ipsilateral motor nuclei (HAGBARTH 1952) as well as to contralateral motor nuclei (MEGIRIAN 1960). In spite of this, a single volley in a skin nerve evokes very similar actions as high threshold muscle and joint afferents to a number of neuronal systems and they have therefore been included among the FRA. This investigation has been limited to the crossed actions evoked by stimulation of the sural nerve and the intention has not been to give a complete analysis of the crossed actions of cutaneous origin. Usually volleys in the sural nerve gave the same modality of crossed actions as volleys from the other FRA. This is illustrated in Fig. 19 H. Fig. 29 C and G, Fig. 30 E, and Fig. 31 C and F. Only to 4 motor nuclei in 3 of 17 experiments did volleys in cutaneous nerves and volleys in the other FRA evoke actions of opposite modality.

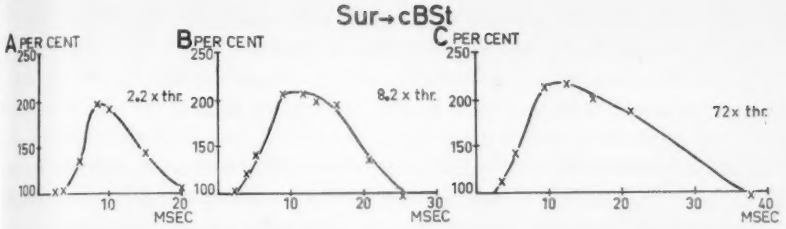

Fig. 24. Crossed actions of a conditioning volley in the sural nerve on the BSt monosynaptic reflex recorded peripherally as in Fig. 22. The intervals between conditioning and testing stimuli are given on the abscissa. Procedure and conventions as in Fig. 1.

The central delay for the crossed actions evoked by volleys in cutaneous nerves was often much shorter (2.5 msec) than for the actions from the other FRA (3.5—6 msec) (cf. also Fig. 19). This short latency is also apparent in Fig. 24 where it has been estimated to be of this order. In this figure the actions of a conditioning volley in the sural nerve are shown on the contralateral BSt test reflexes, peripherally recorded. Graded stimulation revealed that activity in the largest fibres were responsible for a major part of the crossed facilitation (curves in A and B), whereas impulses in thinner fibres only prolonged the facilitatory actions.

Discussion

As mentioned in the introduction to this chapter it was found that actions from the flexor reflex afferents (FRA) converge to a number of neuronal systems and that in all cases the receptive field is very wide. In the present series on acute spinal animals the various afferent systems comprising the FRA almost invariably evoked the same actions in any given contralateral motor nucleus and also in this case there was convergence from a wide receptive field; in particular the convergence of crossed actions from extensor and flexor muscles should be noted. In the same preparation the FRA almost invariably gave the same modality of action to all extensor nuclei. The only flexor nucleus regularly investigated was BSt. When DP occasionally was tested (3 experiments), its receptiveness was the same as that of BSt, but in all three cases the effect was excitation to both these flexors. It can therefor not be excluded that BSt and DP may have a different receptiveness in acute spinal animals as was found in chronic spinal animals (table 2 B, p. 41).

In the different experiments on acute spinal animals the effects from the FRA occurred in the following combinations to extensors and flexors (BSt):

1) excitation to extensor and inhibition to flexor (BSt) nuclei,
2) excitation to both extensor and flexor nuclei,
3) inhibition to extensor and excitation to flexor nuclei,
4) inhibition to both extensor and flexor (BSt) nuclei.

Combinations with excitation to extensor nuclei, 1) and 2), were frequently met with (table 2 A, p. 41) and were the only variations observed in chronic spinal animals (table 2 B). In the acute spinal preparations the pattern to some extent depended on the interval after transection of the cord but after a few hours the pattern generally remained unchanged although a reversal of the action was occasionally observed. There was no difference between 'high' and low acute spinal animals.

The fact that volleys evoked by electrical stimulation of a nerve trunk can give effects of opposite sign is in itself not suprising, and reversal of reflex actions have been described under a variety of experimental conditions (cf. GRAHAM BROWN 1912, PI-SUÑER and FULTON 1929, CREED et al. 1932, JOB 1953). For the interpretation of the present results, recent findings on actions by the FRA on ipsilateral motor nuclei should be considered. In spinal animals in good condition the FRA give excitatory action to flexor and inhibitory action to extensor motor nuclei. Inhibitory action to flexor nuclei is often found, and, though more exceptionally, also excitatory action to extensor nuclei (ECCLES and LUNDBERG 1959 a, PAINTAL 1961, HOLMQVIST and LUNDBERG 1959 b, 1961). For a number of reasons (HOLMQVIST and LUNDBERG 1961) it has been postulated that the same afferent fibres have two interneuronal pathways with opposite end effects to the same ipsilateral flexor motoneurones. The functional organization of the ipsilateral and contralateral effects from the FRA owns so many characteristics in common, not least with respect to their supraspinal control (cf. next chapter), that it seems reasonable to suggest the same explanation for the crossed pathways i.e. two interneuronal pathways from the same afferent fibres with opposite end effect on contralateral motoneurones. The variability in crossed spinal effects from the FRA, often without reciprocity, would suggest a more labile relationship between these interneuronal paths than on the ipsilateral side, as could perhaps be expected with longer interneuronal chains.

As volleys in the FRA evoke ipsilateral actions with a pattern in conformity with that of the flexion reflex (SHERRINGTON 1910) the question arises, whether the crossed actions from the FRA also can be correlated with crossed reflex movements. The crossed extension reflex with reciprocal actions on extensor and flexor nuclei is well known and SHERRINGTON

(1906, 1910) found that this reflex could be evoked by stimulation of muscle as well as skin nerves, and he has actually stated that 'the afferent nerves which evoke crossed extension include all those which evoke ipsilateral flexion'. GRAHAM BROWN (1911) first emphasized that crossed flexion also could go together with the ipsilateral flexion reflex (cf. also SHERRINGTON 1898). One reason that he observed this more frequently than SHERRINGTON may have been that he studied reflex contractions in ankle muscles whereas SHERRINGTON mainly used knee muscles. In a joint study of exceptional reflex reactions GRAHAM BROWN and SHERRINGTON (1912) found that crossed flexion, though rare, occurred more often at the ankle than at the knee. This is interesting since in the present investigation a similar difference has been noted in the crossed receptiveness of BSt and DP in chronic spinal cats. To some extent the type of crossed effect obtained may also be due to the time elapsed after spinal transection. MCCOUCH et al. (1935) found that initially (from 20 min to 24 hours after the transection) stimulation of the skin or of a nerve invariably yielded crossed flexion, which reflex after a transient period with mixed movements at various contralateral joints changed into crossed extension. In the present study one observation in the same direction was made; the variable pattern found in acute spinal animals was stabilized in chronic cats, there was always facilitation to contralateral extensor nuclei, although the effect to the contralateral BSt nucleus could be inhibition or excitation.

Thus there are similarities between the crossed reflex actions studied in earlier investigations and the present one, and it might be assumed that essentially we are dealing with the same phenomenon. There are, however, also discrepencies in the results as well as the experimental procedure, as will be discussed.

In many of the earlier investigations the muscle tension was recorded in preparations with the gamma-loop left intact and crossed actions to gamma motoneurones are known to exist (HUNT 1951), but the crossed extensor reflex as well as the crossed flexor reflex have been observed in de-afferented muscles (GRAHAM BROWN 1911, 1912, 1914).

In SHERRINGTON's (1906, 1910) experiments reciprocal actions to extensor and flexor nuclei were a constant feature of the crossed extension reflex. As described above this was not always found for the crossed effects from the FRA. It is not known to which extent the reciprocal inhibition of flexor nuclei in SHERRINGTON's experiments may have been a recurrent Renshaw inhibition caused by discharges in extensor motoneurones on the testing side (cf. RENSHAW 1941, ECCLES et al. 1954, GRANIT, PASCOE and STEG 1957, but also WILSON 1959, WILSON et al. 1960). Neither is it known to

which extent the nociceptive systems have been activated in the different investigations and whether impulses in these fibres more constantly can give rise to the reciprocal actions of the crossed extensor reflex.

In the present investigation the latencies of the crossed effects evoked from the FRA were relatively short. SHERRINGTON (1910, cf. also CREED et al. 1932) found very much longer latencies for the crossed extension reflex, and repetitive stimulation was usually necessary to evoke the reflex. In later investigations by ECCLES and GRANIT (1929) and FORBES and CATTELL (1924) considerably shorter latencies were found. It is important to remember that most of these experiments were made on decerebrate cats and the results are therefor not directly comparable with effects observed in spinal cats. Crossed reflex pathways are suppressed in the decerebrate state (cf. next chapter), and one reason for the long latencies may have been that temporal facilitation was necessary to overcome the suppression from supraspinal centres. However, in chronic spinal 'deafferented' cats MATTHES and RUCH (1933) have found a crossed reflex contraction in soleus evoked by a single stimulus after a latency of a similar order as that now found for the crossed facilitation.

Summary

In spinal cats single volleys in skin, high threshold joint and high threshold muscle afferents evoke similar actions in any given contralateral motor nucleus. The following minimal central delays were found for volleys in high threshold muscle afferents, 3—4 msec; in high threshold joint afferents, 5 msec; and skin afferents 2.5 msec. The duration of the action was about 25 msec.

In acute spinal animals motor nuclei of synergic muscles (extensors or flexors) usually received the same modality of action. However, the pattern of actions varied in different preparations, and all four possible variations of actions were met with:

1) facilitation to extensor and inhibition to flexor (BSt) nuclei,
2) facilitation to both extensor and flexor nuclei,
3) inhibition to extensor and facilitation to flexor nuclei,
4) inhibition to both extensor and flexor (BSt) nuclei.

The first two types were common in acute spinal animals and in chronic spinal cats the only types observed.

In chronic spinal cats DP received excitation regardless whether BSt was excited or inhibited.

The variability in the pattern of crossed actions has been discussed in connection with previous investigations on crossed reflexes.

Chapter IV

Supraspinal control of the crossed actions evoked from the flexion reflex afferents

Introduction

Information regarding supraspinal control of the ipsilateral reflex actions by the FRA (flexor reflex afferents) has been derived from a comparison of these actions in the decerebrate and in the spinal states. SHERRINGTON and SOWTON (1915) demonstrated with accurate methods that the flexor reflex was easier to elicit in the spinal than in the decerebrate animal. They assumed that this was due to higher excitability of flexor motoneurones in the spinal than in the decerebrate state. FULTON (1926) suggested that in the decerebrate state inhibition of the interneurones transmitting these actions may be another explanation and later investigations have shown that there is such a tonic inhibition of interneurones of the flexion reflex pathways in the decerebrate state (JOB 1953, ECCLES and LUNDBERG 1958, 1959 b, KUNO and PERL 1960).

This tonic inhibition of interneurones of ipsilateral reflex arcs can act independently of the cerebellum and the vestibular nuclei, hence, it can be differentiated from the tonic control responsible for decerebrate rigidity (HOLMQVIST and LUNDBERG 1959 a). The centers responsible for the tonic inhibitory control of flexor reflex pathways are located medially in the brain stem and their descending pathways are located in the dorsal part of the lateral funiculi and from each side a bilateral effect is exerted (HOLMQVIST and LUNDBERG 1959 a). Experiments with lesions at different levels in the lower reticular formation have revealed a differential control of inhibitory pathways to extensor motoneurones and of excitatory to flexor motoneurones. A lesion in the lower pons releases inhibitory pathways to ipsilateral extensor motor nuclei whereas a more caudal lesion is necessary for release of the excitatory pathways to flexor motoneurones. In addition it has been found that a low pontine lesion also releases an inhibitory pathway from the FRA to ipsilateral flexor motoneurones (HOLMQVIST and LUNDBERG 1959 b, 1961). A similar organization has now been established for the supraspinal control of the crossed actions from the FRA. The supraspinal control of the decerebrate preparation will be described in section A. Section B deals with the effects of a low pontine lesion.

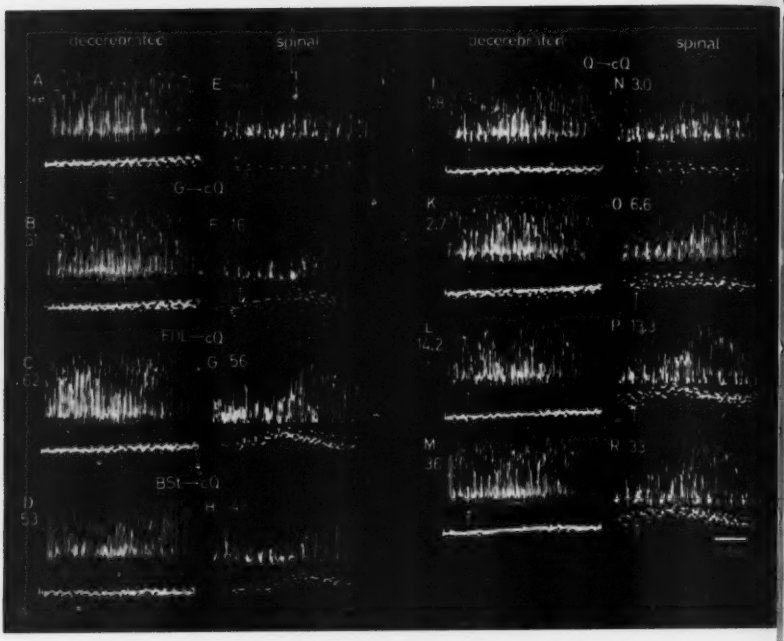

Fig. 25. The crossed actions on the Q monosynaptic reflexes of single conditioning volleys in the various nerves indicated. Record A—D and I—M were obtained after intercollicular section and E—H and N—R after section of the cord in L_2. The same experiment as in Fig. 26—28. Procedure and conventions as in Fig. 3. Some records are retouched.

Results

A. *Comparison of crossed actions in the decerebrate and spinal states*

In these experiments on decerebrate cats (intercollicular section) the effects of conditioning volleys on contralateral monosynaptic reflexes were studied in the decerebrate state and compared with the effects subsequently obtained after section of the cord in L_2 or after a medial lesion at obex (cf. p. 35, chapter III) both giving a release to the spinal state.

In the decerebrate state there was the same absence of crossed group I actions on monosynaptic test reflexes, as has been found in the spinal state (cf. chapter II). When the group I volley displayed the separation in the I a and I b components it was also ascertained that neither the I a nor the I b volley evoked any crossed effect. This is exemplified in Fig. 25 where the monosynaptic reflex from Q was conditioned from the

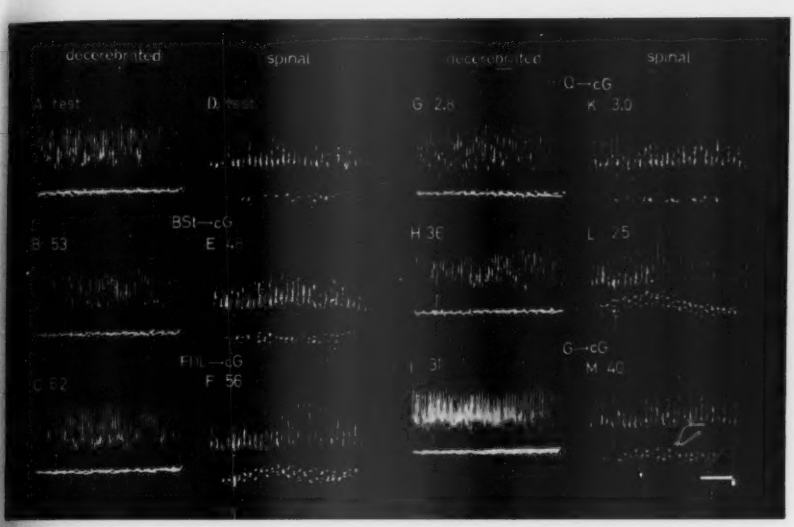

Fig. 26. Crossed actions on the G monosynaptic reflexes of single conditioning volleys in the various nerves indicated, in the decerebrate and spinal states. The same experiment as in Fig. 25, 27 and 28. Procedure and conventions as in Fig. 3 and 25. Some records are retouched.

contralateral Q nerve with a Ia volley (record I) and a just maximal group I volley (record K). Neither were there any crossed effects by group I volleys after section of the cord (record N, cf. chapter II). For control ipsilateral group I effects were sometimes recorded in the decerebrate state and potent Ia reciprocal inhibition was found (cf. Fig. 28 B).

A representative survey of the difference between crossed actions evoked by a conditioning volley in high threshold muscle afferents in the decerebrate and spinal states are given in Fig. 25—28. Each figure represents the actions to one motor nucleus and the records are arranged in pairs, with the left obtained before and the right after transection of the cord in L_2.

Fig. 25 illustrates the effects on the contralateral Q test reflexes, shown unconditioned in A and E. Before spinal section volleys in high threshold muscle afferents from G, FDL, BSt and Q (records B—D, L and M) did not give any crossed actions but after section of the cord corresponding volleys gave large facilitatory effects (records F—H, P and R). For the Q nerve this phenomenon is shown at different stimulus strengths, and for all stimulus strengths up to 36 times threshold (I—M), there was the same lack of actions in the decerebrate state in spite of a good segmental

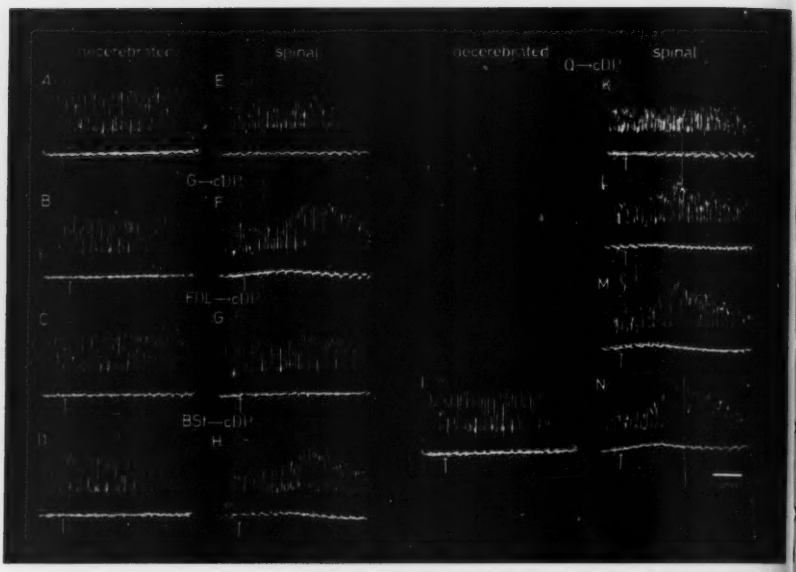

Fig. 27. Crossed actions on the DP test reflexes of single conditioning volleys in the various nerves indicated, in the decerebrate and spinal states. The same experiment as in Fig. 25, 26 and 28. Procdure and conventions as in Fig. 3 and 25.

condition of the cord, indicated by the low threshold for the crossed effect after spinal section. Thus, already a group II volley, at 6.6 times threshold, evoked significant facilitation (O), which increased when group III fibres were activated (P and R). It is suggested that the suppression of actions in B—D, L and M is due to a tonic inhibition from supraspinal centers on the pathways mediating the actions from the FRA.

The same features were also found to the other contralateral extensor nuclei investigated, G (Fig. 26) and FDL (not illustrated). In no instance was there in this series any sign of crossed actions by impulses in high threshold muscle afferents in the decerebrate condition (Fig. 26 B, C, H and I), although pronounced crossed facilitation to contralateral G (Fig. 26 E, F, L and M) and to contralateral FDL was found in the spinal state.

Effects on crossed pathways to flexor nuclei are illustrated in Fig. 27 and 28. In Fig. 27 there is similarly no crossed effect to DP by volleys in high threshold muscle afferents in the decerebrate state (B—D and I), but release of facilitation in the spinal state (F—H and L—N). On the

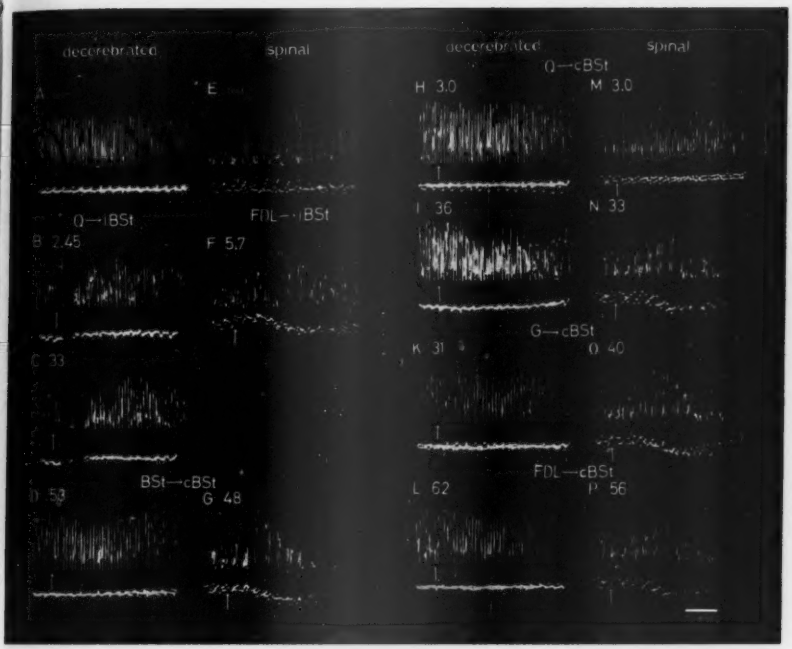

Fig. 28. Crossed actions on the BSt monosynaptic reflexes of single conditioning volleys in the various nerves indicated, in the decerebrate and spinal states. The same experiment as in Fig. 25—27. Procedure and conventions as in Fig. 3 and 25.

other hand, in Fig. 28 there is in the decerebrate state no crossed effect to BSt from BSt (D) and FDL (L) but crossed inhibition from Q (I) and probably also a trace from G (K). Nevertheless after section of the cord the facilitatory effects from Q and G (N and O) resembled those from the other nerves (G and P). This inhibition from contralateral Q (I) is of special interest since it was found that a corresponding volley in the ipsilateral Q also inhibited the BSt test reflex. This is shown in record C, where the first inhibitory phase was caused by impulses in the I a afferents (cf. record B), whereas the additional later inhibitory phase was due to activity in high threshold afferents. Such an inhibitory action from FRA to ipsilateral flexor nuclei is occasionally met with in decerebrate preparations (cf. ECCLES and LUNDBERG 1959 b, Fig. 2; HOLMQVIST and LUNDBERG 1959 a, Fig. 3 and 5; HOLMQVIST and LUNDBERG 1961). The bilateral inhibitory effects from Q have been interpreted as due to a partial release from

the otherwise complete blockage in the decerebrate state of pathways mediating inhibitory actions from FRA (cf. section B in this chapter).

It should be noted that the sizes of the unconditioned test reflexes before and after transection of the cord do not reflect corresponding changes in alpha excitability because double volleys were often used to evoke test reflexes (cf. methods). After section of the cord the excitability was usually increased in flexor and decreased in extensor motoneurones. In the present investigation it was attempted to use test reflexes of equal size before and after section of the cord as for the DP test in Fig. 27 (A and E) but sometimes this was not possible. In Fig. 25, 26 and 28 the test reflexes are smaller in the spinal than in the decerebrate state. The reason is that in these experiments double stimuli could not be used for evoking the test reflexes after section of the cord. This may be connected with the often marked spontaneous fluctuations found in the spinal state (presumably because of the release of reflex arcs from supraspinal control). Therefore it was difficult to keep the first test volley subliminal particularly when a conditioning volley gave facilitation but sometimes also for the unconditioned test reflexes. In several experiments it was, however, controlled that conditioning volleys in the FRA had no action in the decerebrate state even when smaller test reflexes were used.

Also Fig. 29 is from a decerebrate preparation, which shows not only the suppression of crossed spinal actions evoked by volleys in high threshold muscle afferents on contralateral G (A and B) and BSt (E and F) test reflexes but also of the crossed actions from the other FRA, namely of cutaneous (C and G) and articular (D and H) origin. The curves in G show that neither at weak (■) nor at strong (●) stimulus strengths were there any crossed effects from the sural nerve to BSt in the decerebrate state, in spite of quite pronounced facilitatory actions (□, ×) after section of the cord. This is interesting because even in decerebrate preparations with very effective control of actions to other pathways activated by the FRA there is usually from the sural nerve an early ipsilateral facilitatory action both to flexors and extensors which is evoked by impulses in large cutaneous afferents (HOLMQVIST and LUNDBERG 1961). In the experiment illustrated in Fig. 29 there was also in the decerebrate state such ipsilateral facilitatory action to BSt from the largest fibres in the sural nerve and exclusively from these fibres. In 11 of 13 decerebrate cats there was complete suppression of crossed effects from the sural nerve. In 7 of these cats, there were ipsilateral facilitatory actions in the decerebrate state from the sural nerve as has been described for the preparation in Fig. 29. (In the remaining 4 experiments the ipsilateral effect was not controlled.) However, in 2 experiments there was a slight crossed facilitatory action from the sural nerve, in one case to both BSt and G in the other only to G. In the former experiment the threshold at which the effect appeared

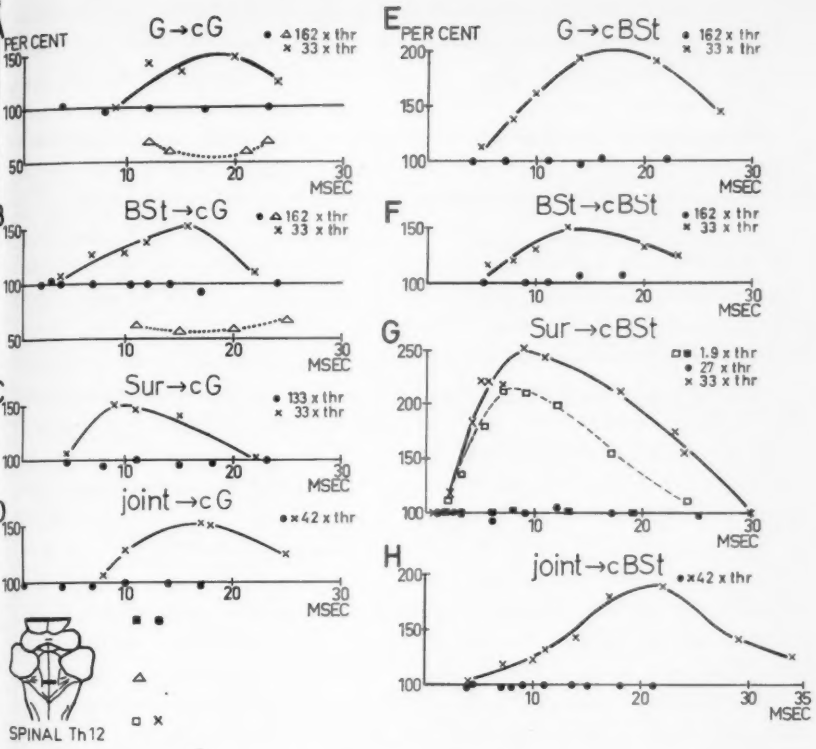

Fig. 29. Crossed actions of single conditioning volleys in the various nerves indicated on the monosynaptic reflexes from G (A—D) and from BSt (E—H) in the decerebrate state, (■●) after a pontine lesion (△), as indicated in the schematic drawing, and after spinal section in Th_{12} (□×). Procedure and conventions as in Fig. 1.

was measured and was found to be high. (The other experiment was not analysed in this respect.) It is possible that the ipsilateral cutaneous effects which escape the control in the decerebrate state should not be included among the actions of the FRA, but other explanations cannot be excluded.

The decerebrate cat illustrated in Fig. 29 was cerebellectomized (cf. also Fig. 30 and 31), whereas in the experiments illustrated in Fig. 25—28 the cerebellum was left intact. No difference has been observed between these two types of preparations (cf. HOLMQVIST and LUNDBERG 1959 a).

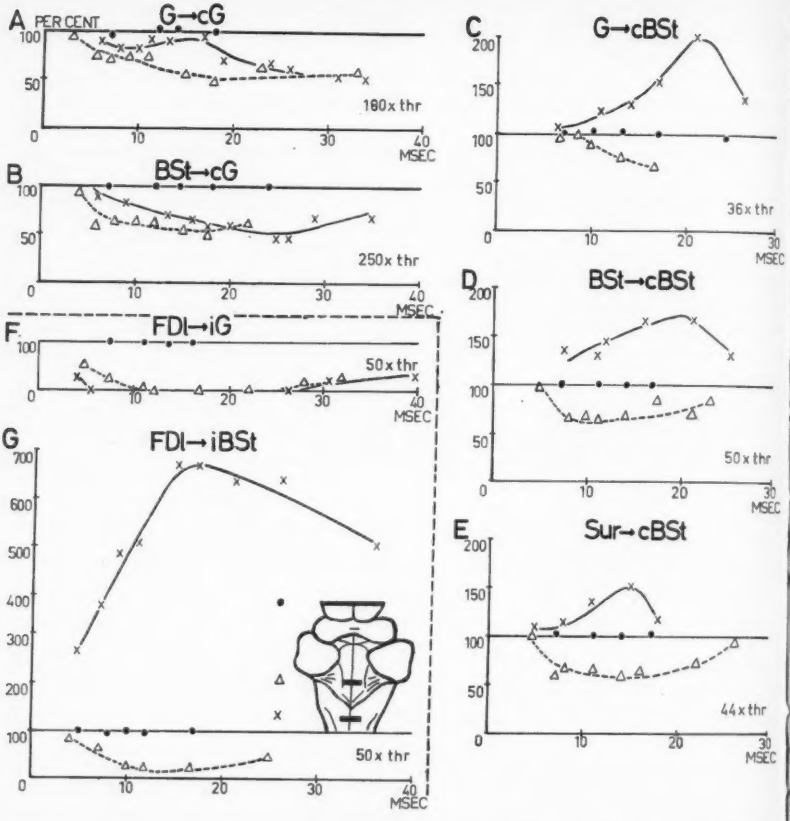

Fig. 30. Contralateral (A—E) and ipsilateral (F and G) actions on the G (A, B and F) and on the BSt (C—E and G) test reflexes evoked by single conditioning volleys in the various nerves indicated after lesions given in the schematic drawing. Procedure and conventions as in Fig. 1 and 29.

B. *Effects of lesions in the brain stem on crossed actions*

In the present investigation the actions from the FRA to motor nuclei of both sides were compared at successive more caudal lesions in the brain stem. It was found that a low pontine lesion at the level indicated in the schematic drawing of Fig. 30, which released inhibitory actions (△) to the ipsilateral G (curve in F) and BSt (curve in G) concom-

itantly released inhibitory actions to the contralateral G (curves in A and B) and BSt (curves in C—E). This was found for actions by all FRA, high threshold muscle afferents (A—D), skin afferents (E) and high threshold joint afferents (cf. Fig. 31 G). After a more caudal lesion there was also release of facilitatory actions by the FRA. It was found that a medial lesion in the region of obex (×) was as effective as a complete transection of the cord, and henceforth, this preparation will be regarded as spinal (cf. p. 35).

In Fig. 30 the crossed spinal pattern was inhibition to extensors and facilitation to flexors, which is one of the spinal patterns described in chapter III. In a similar experiment, partly illustrated in Fig. 29, a low pontine lesion (△) was also followed by a general inhibition which is shown only for contralateral G (curves in A and B). In the spinal state there was in this case a reversal to general facilitation of contralateral extensor and flexor test reflexes (×). In the experiment illustrated in Fig. 31, on the other hand, the general inhibition revealed by the pontine lesion (△) remained on the contralateral side after a lesion at obex (×) and transection of the cord (not illustrated).

In low pontine preparations a comparison of ipsilateral and contralateral inhibitory effects from the FRA has revealed, that the effects were always more marked ipsilaterally. On the ipsilateral side this lesion gives an almost complete release of the inhibitory pathways to extensor motoneurones and concomitantly a release of inhibitory paths to flexor motoneurones from the FRA (HOLMQVIST and LUNDBERG 1959 b, 1961). The ipsilateral inhibition to flexor motoneurones is often weak but in the experiments illustrated in Fig. 30 and 31 there was on the ipsilateral side almost complete inhibition of the BSt test reflexes from FDL (Fig. 30 G and Fig. 31 I). On the contralateral side the test reflexes were seldom reduced by more than 50 per cent (Fig. 30 A—E, Fig. 31 A—G). These crossed inhibitory effects after a low pontine lesion could only in one experiment be evoked by volleys in group II muscle afferents (conditioning stimulus strength 5 times threshold); in 9 other experiments group III volleys were required. Probably the absence of crossed group II effects after the low pontine lesion in most of the experiments has no special significance, because absence of group II effects is also common for the ipsilateral actions after a low pontine lesion (HOLMQVIST and LUNDBERG 1961).

Both in Fig. 30 and 31 the crossed inhibitory actions were larger after a low pontine lesion than in the spinal state. Possibly this may be due to spinal shock but another factor may be release of excitatory paths (cf. chapter III). By intracellular recording from motoneurones it has been

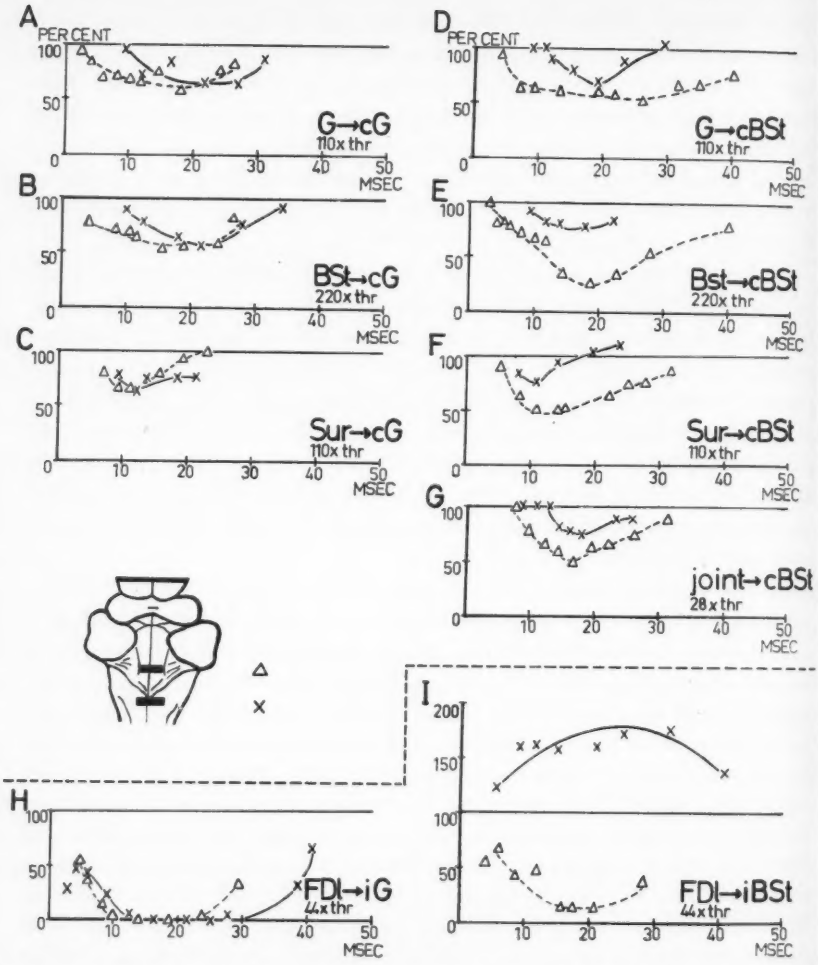

Fig. 31. Contralateral (A—G) and ipsilateral (H and I) actions on the G (A—C and H) and on the BSt (D—G and I) monosynaptic test reflexes evoked by single conditioning volleys in the various nerves indicated after lesions given in the schematic drawing. Procedure and conventions as in Fig. 1 and 29.

confirmed that impulses in the FRA may evoke excitatory or inhibitory synaptic actions in motoneurones of the same contralateral nucleus, and also that individual motoneurones may receive both these crossed actions (HOLMQVIST and LUNDBERG, unpublished).

Discussion

It has been established that in the decerebrate state single volleys in the FRA usually do not evoke any actions on contralateral monosynaptic test reflexes, but after a medial lesion at obex or transection of the cord there is a release of crossed spinal actions, such as were described in chapter III. The suppression of crossed actions from the FRA in the decerebrate state much resembles what has been found for their ipsilateral actions (ECCLES and LUNDBERG 1959 b), and it seems reasonable to suggest that also interneurones of the paths from the FRA to contralateral motoneurones are tonically inhibited from the brain stem in the decerebrate state in a similar fashion, as has been concluded for their ipsilateral actions. No crossed group I effects were observed in the decerebrate state in this series, but since there were no effects after section of the cord this finding leaves the question open, whether there is a similar supraspinal control of crossed group I pathways as has been found for the ipsilateral Ib pathways (ECCLES and LUNDBERG 1959 b).

In decerebrate cats SHERRINGTON (1910) found that spinal transection gave an immediate fall in threshold and volume of the ipsilateral flexion reflex, but a rise in threshold and fall in supraliminal response of the crossed extensor reflex. As suggested by SHERRINGTON (1910), this rise in threshold of the crossed reflex may be due to a fall in excitability of alpha motoneurones to extensors following the spinal transection. Another possibility is that crossed reflex excitation of gamma motoneurones (HUNT 1951, GRANIT 1955) may be different in the decerebrate and spinal states. This possibility deserves special attention since the decerebrate rigidity is maintained by the gamma-loop (cf. GRANIT 1955).

Further evidence of parallelism in supraspinal control of ipsilateral and contralateral reflex pathways from the FRA has been given in the experiments on decerebrate cerebellectomized animals with a low pontine lesion. This lesion, which releases inhibitory reflex pathways from the FRA to ipsilateral extensor as well as flexor motoneurones (HOLMQVIST and LUNDBERG 1959 b, 1961), also gives release of inhibitory paths from the FRA to contralateral extensor and flexor motor nuclei, whereas a more caudal lesion is necessary to release excitatory pathways to both sides.

For the ipsilateral reflex actions from the FRA it has been postulated that supraspinal centres differentially can control actions to flexor and extensor motoneurones and also that they can select between an excitatory and an inhibitory channel to flexor motoneurones (HOLMQVIST and LUNDBERG 1961). On similar grounds it is suggested that supraspinal centres differentially may govern FRA pathways to contralateral motoneurones.

This suggestion may help to explain the puzzling findings in spinal animals, in which FRA volleys under apparently the same conditions but in different preparations can evoke opposite crossed effects in the same motor nucleus. Possibly the supraspinal centres may select suitable inhibitory or excitatory channels to contralateral motoneurones and it is not necessary to assume that reciprocal innervation of flexor and extensor nuclei is maintained in this selection.

It should, however, be noted that the experiments with pontine lesions have revealed only that the centres controlling inhibitory and excitatory pathways have a different localization in the brain stem. The degree of functional freedom between these centres cannot be decided by experiments of the present type. It is neither possible to make any suggestions about the functional linkages between these controlling systems located at the same brain stem level. Even if there are great resemblances in the release from supraspinal control of ipsilateral and crossed reflex arcs after lesions at various brain stem levels (cf. Fig. 28) it is nevertheless possible that the supraspinal centres may control these reflex arcs independently.

Summary

It has been established that the pathways of the crossed actions from the flexor reflex afferents (FRA) are under a similar supraspinal control as has been found for the corresponding ipsilateral paths.

In decerebrate cats single volleys in skin, high threshold joint and muscle afferents have no actions on contralateral monosynaptic test reflexes, but after a medial lesion at obex or transection of the cord in the upper lumbar region a release of crossed spinal actions from these afferent systems occurs. It is postulated that in the decerebrate state there is a supraspinal tonic inhibitory control of the interneurones mediating crossed actions from the FRA.

There is evidence of a separate control of pathways mediating the facilitatory and inhibitory crossed actions because a medial lesion in the low pontine reticular formation releases only inhibitory actions from the FRA to contralateral flexor nuclei as well as to extensor nuclei. A more caudal lesion is necessary to release the crossed facilitatory actions.

Comments and Summary

This investigation deals with the crossed spinal reflex actions to alpha motoneurones from various myelinated afferents in the hindlimb of the cat.

It has not been possible to distinguish between crossed effects evoked by impulses in I a and I b afferents, but to a certain extent the experimental series on crossed group I effects must be considered as introductory to further experiments with intracellular technique. Recording of synaptic potentials in individual motoneurones presumably gives a better chance to utilize the slow and fast components of the group I volley. At the same time the present findings are of importance for the future analysis. It has now been revealed that repetitive stimulation is required to evoke clear cut crossed group I action and a quantitative frame for actions expected in various motor nuclei has been erected. Of particular interest for further analysis of the crossed group I actions is:

1) The source of the crossed excitation between extensors.
2) The absence of crossed inhibitory actions between extensors.
3) The difference in crossed receptiveness of DP and BSt as well as the differencies in crossed actions evoked by volleys from these muscles.
4) The possibility of crossed presynaptic inhibition. Inhibitory group I effects may be due to presynaptic inhibition (FRANK and FUORTES 1957, ECCLES, ECCLES and MAGNI 1960, ECCLES 1961) and such effects will be difficult to disclose without intracellular recording.

The investigation of actions evoked by volleys in the FRA (group II and III muscle, skin, and high threshold joint afferents) perhaps permits more definite suggestions. Contralateral motoneurones provide a new neuronal system showing convergence of effects from group II and III muscle afferents, from high threshold joint afferents and skin afferents and the concept of the unity of actions evoked by the FRA has thereby been strengthened (cf. ECCLES and LUNDBERG 1959 a, LUNDBERG 1959, HOLMQVIST, et al. 1960).

In view of the relative constancy of the crossed extensor reflex and the well established concept of double reciprocal innervation it was surpris-

ing that volleys in the FRA could evoke either excitation or inhibition in flexor and extensor nuclei and that the combination with facilitation to both extensor and flexor nuclei was particularly common. In this case preliminary experiments with intracellular recording have revealed inhibitory and excitatory synaptic potentials in flexor as well as extensor motor neurones (HOLMQVIST and LUNDBERG, unpublished). The possibility remains that these non reciprocal crossed actions are evoked by afferents with different receptive function but another suggestion seems more likely i.e. that the same afferent fibres may have two alternative paths to a given contralateral motor nucleus. This has been postulated to account for the dual actions from the FRA to flexor nuclei on the ipsilateral side (ECCLES and LUNDBERG 1959 a, HOLMQVIST and LUNDBERG 1959 b, 1961) and the present suggestion for the contralateral connections is given by analogy. On the ipsilateral side the reciprocal flexor reflex actions from the FRA are very dominant in spinal preparations in good condition but apparently there is a more labile relationship between the corresponding crossed actions. This may be due merely to longer internuncial chains in the crossed paths but it is possible that differential actions on the contralateral side are more often required in the various reflex movements of the animals.

The experiments on the supraspinal control of crossed actions were concerned exclusively with the actions from the FRA and have shown a parallelism with the control of ipsilateral reflex arcs (ECCLES and LUNDBERG 1959 b, HOLMQVIST and LUNDBERG 1959 b, 1961). There is likewise suppression of action in the decerebrate state and release of inhibition to both contralateral extensor and flexor motor nuclei after a low pontine lesion. Thus the low pontine preparation is characterized by general inhibition with loss of reciprocal and double reciprocal innervation. A more caudal lesion in the medulla is necessary to release crossed excitatory actions from the FRA.

It is true that some of the crossed spinal effects disclosed in this investigation were weak but this does not necessarily mean that their functional significance is negligible since some reflex arcs may receive facilitation from supraspinal centres. It has recently been shown that interneurones of ipsilateral reflex arcs are facilitated by impulses in the pyramidal tract (LUNDBERG and VOORHOEVE 1961).

The work was originally suggested by Professor Anders Lundberg. I wish to express my sincere gratitude for his stimulating advice and valuable help. Thanks are due to Mr. E. Eide, Miss Karin Ebbesson and Miss Solveig Jeppsson for much appreciated technical assistance.

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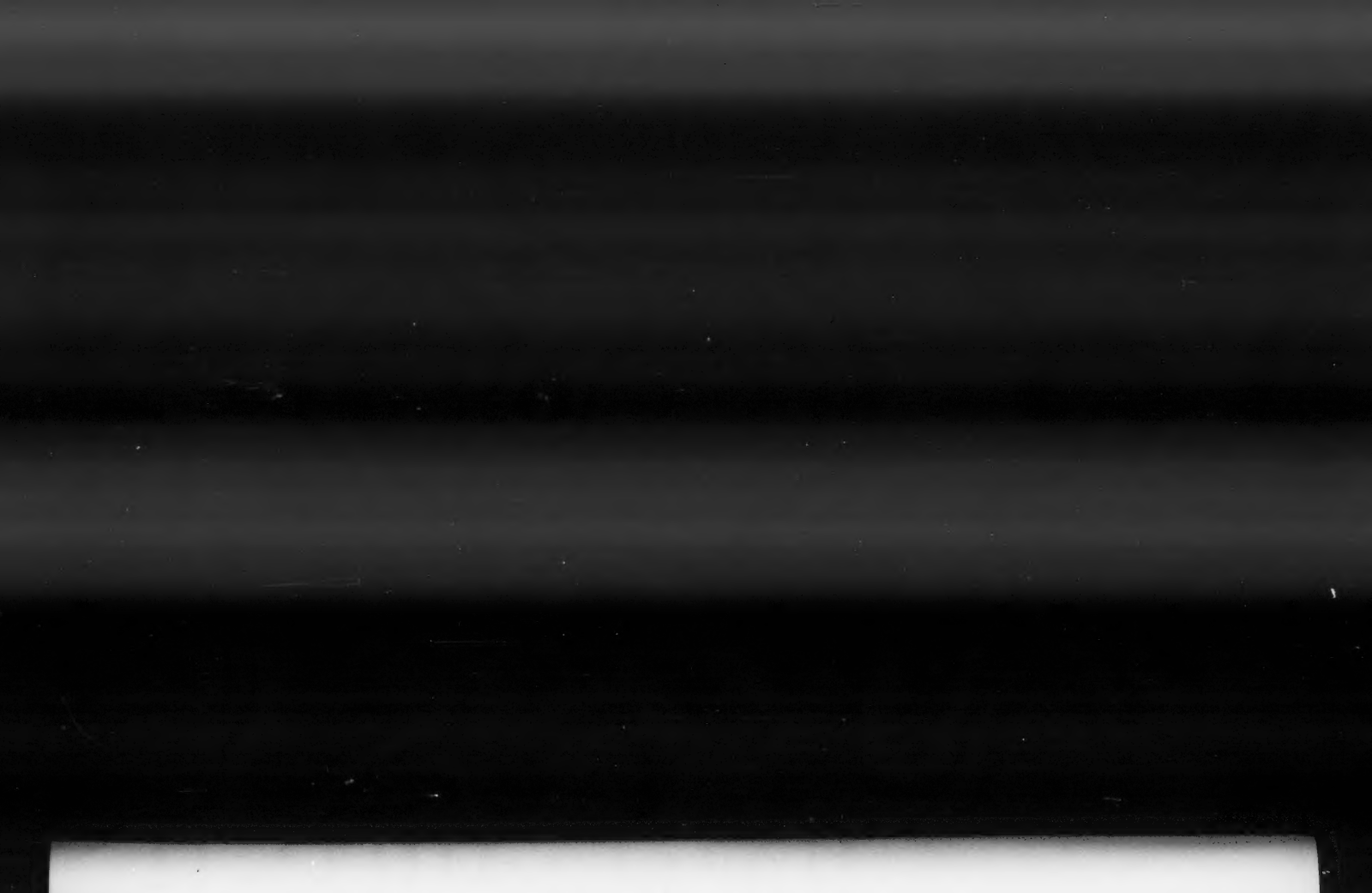
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